DISSERTATION

ASSESSING GRASSLAND SENSITIVITY TO GLOBAL CHANGE

Submitted by

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ABSTRACT

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Intensification of the global hydrological cycle with atmospheric warming is expected to substantially alter precipitation regimes, and due to the tight functional relationship between precipitation and net primary productivity (NPP), these changes in climate will have large impacts on multiple NPP-linked ecosystem services such as forage production and carbon storage. At regional scales, the sensitivity of aboveground NPP (ANPP) to variation in annual precipitation increases with decreasing site-level ANPP, with this variation in sensitivity is thought to be related to turnover of plant communities over the precipitation gradient. Site-level ANPP responses are not expected to conform to regional patterns until plant communities shift, resulting in differential short- vs. long-term ANPP responses to chronically altered precipitation amounts. Although studies in grasslands have quantified site-level sensitivities of ANPP to altered precipitation amount, we lack equivalent knowledge for responses of belowground net primary productivity (BNPP) and total NPP. This will be especially important as simultaneous global change factors occur (e.g., increased fire frequency) and interact with climate change drivers to influence NPP and ecosystem services.

My dissertation examines ecosystem sensitivity to altered precipitation amounts and patterns, how changing plant communities alter this sensitivity, and how this impacts various ecosystem services by addressing the following questions: (1) How do plant species and functional compositions control ecosystem sensitivity to altered precipitation regimes? (2) Does belowground sensitivity mirror that aboveground? And (3) What are the consequences of differential ANPP and

BNPP sensitivity on biogeochemical processes in the presence of annual fire regimes? In my second chapter, I show how functional types (C_3 versus C_4 graminoids) can alter regional patterns of sensitivity to annual precipitation through differences in the timing of growth. I also show that ANPP and BNPP sensitivities can differ, but that it likely depends on vegetation and/or other attributes of an ecosystem. In chapter three, I focus on how shifts in plant species abundances, even within the same functional type, can alter sensitivity to extreme, chronic increases in precipitation. The shift in sensitivity was, again, not in agreement with regional patterns of sensitivity. Lastly, chapter four shows that the differential sensitivity of ANPP and BNPP to long term increases in precipitation can destabilize the carbon and nitrogen sequestration ability of ecosystems in the presence of extreme disturbance regimes also likely to occur in the future. Overall, my dissertation calls into question the predictive ability of regional models of NPP sensitivity under chronic shifts in precipitation amount, at least on short to moderate time scales, and I suggest that incorporation of plant community controls on above- and belowground sensitivity will be better predictors of ecosystem service responses under novel environmental conditions likely to occur in the future.

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Throughout this dissertation, I will extensively use the pronouns *I*, *my,* and *mine*. This is a formal necessity as all scholarly works of this type are thus formatted. However, if it weren't for that, I would be writing *we*, *our,* and *ours*, and so here I would like to acknowledge all the efforts of colleagues, friends and family, without whom, this research never would have been completed.

First and foremost, I would like to thank my advisor, Dr. Alan Knapp, for training me to pursue a career in science, and all the large and small efforts this entailed. I consider myself exceedingly lucky to have been a part of his lab. I would also like to thank my committee, Dr. Joseph von Fischer, Dr. Melinda Smith, and Dr. Eugene Kelly, for guidance through my Ph.D. and for all the wonderful feedback concerning both my science and the development of my professional career. I'd like to thank everyone involved with the Graduate Degree Program in Ecology for making the last 5 years such a great experience. To all those in my lab who have provided feedback on various parts of my research, Dr. David Hoover, Elsie Denton, Melissa Perkins, Jeff Carroll, Robert Griffin-Nolan, Ingrid Slette, and Karie Cherwin thank you. I was also lucky enough to have four amazing collaborators working simultaneously at the Konza Prairie Biological Station who have been so very important for brain storming various project ideas and were always available for emergency field work whenever it arose: Dr. David Hoover (again!), Dr. Sally Koerner, Dr. Meghan Avolio, and Dr. Kim La Pierre. Supporting me from afar were my mom and sister, as they were always stoically available to listen to me complain of soil moisture sensor difficulties and other problems they could only have cared about because I did. To my fiancé, Andrea Borkenhagen, thank you for continually supporting me through this process as well as consistently being a magnificent person to be around. All the people above helped extensively throughout my

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DEDICATION

To my mom,

who, when I complained I would never make it through my undergraduate studies, told me,

“don’t worry, it isn’t a race.”

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CHAPTER 1: INTRODUCTION

Current and past documented warming of the planet will likely continue into the foreseeable future resulting in altered environmental conditions worldwide (IPCC, 2013). In fact, the current time period may soon receive status as its own epoch, the Anthropocene (Crutzen, 2006; Lewis and Maslin, 2015), something typically attributed to periods of time on a geologic scale and separated by significant changes in rock layers (Gradstein et al., 2012; Finney, 2014). Although this designation may seem somewhat presumptuous and perhaps a trifle arrogant, the drivers governing natural processes in the world are changing, and novel situations previously unknown to Earth will continue to arise. As environmental variables continue to change, an important aim of ecology is/will be to provide robust predictions of how ecosystems will respond.

One major effect of a warmer earth is alteration of precipitation regimes across most ecosystems globally (IPCC, 2013). As evaporative forcings increase at the equator, chronic shifts in the amount, pattern, and year-to-year variability of precipitation will occur with the magnitude of effects varying across geographic regions (IPCC, 2013, Greve et al., 2014). Ecosystem function, especially net primary productivity (NPP), is strongly linked to precipitation across the majority of terrestrial ecosystems (Sala et al., 1988, 2012; Huxman et al., 2004; Del Grosso et al., 2008), and changes in NPP can have cascading consequences for numerous ecosystem services. For example, aboveground NPP (ANPP) controls forage availability and habitat quality, while belowground NPP (BNPP) can influence carbon sequestration and erosion control. Therefore, understanding the responsiveness of both ANPP and BNPP to predicted changes in precipitation patterns is of importance. And although broad scale patterns of these sensitivities are useful,

equally important for predicting ecosystem responses to global change is understanding why systems might depart from these general relationships (Knapp et al., 2004).

In much of this dissertation, I focus on patterns and responses of the sensitivity of ecosystem function to altered precipitation regimes. Specifically, I examine the magnitude of primary production responses to given alterations in precipitation regimes (e.g., an *x* change in primary productivity in response to a *y* change in precipitation amount: sensitivity – Fig. 1.1B).

Although spatial models have shown robust relationships between the average ANPP in an ecosystem and its mean annual precipitation (MAP; Sala et al., 1988, 2012; Fig. 1.1A), these correlations are not useful for predicting ecosystem responses to climate change-driven alterations in precipitation on short or moderate time scales. This is due to inherent differences in ecosystem attributes (e.g., plant species composition, edaphic properties) that partially drive this pattern when moving among systems (i.e. across space; Lauenroth and Sala, 1992). Alternatively, temporal models relate annual primary productivity in a single ecosystem to the amount of rainfall coming in a particular year, and are almost always shallower in slope than the spatial model due to ecosystem attributes constraining the system's response to changes in precipitation (Burke et al., 1997; Fig. 1.1B). These models are useful for predicting short-term productivity responses to chronically altered precipitation amounts and the slope of this relationship can be thought of as the sensitivity of the system (Fig. 1.1B). This is because these models describe the magnitude of response that is likely to occur with changes in precipitation when all other ecosystem attributes are held constant. However, the sensitivity of ecosystems will likely change along with chronically altered precipitation, and spatial models of sensitivity across precipitation gradients have been constructed to inform how this sensitivity might shift under climate change (Huxman et al., 2004; Sala et al., 2012). These large-scale relationships show that sensitivity is typically higher in more

xeric systems and lower in mesic systems. This phenomenon has been proposed to be due to co-limitation by resources such as nitrogen (Huxman et al., 2004; Fig. 1.1C1) so that, during wet years in mesic systems, productivity is not constrained by water availability, but by the other limiting resource (or a release of co-limitation during wet years as you move to more xeric systems; Fig. 1.1C2). However, like the ANPP-MAP spatial relationship, this model of sensitivity suffers from the assumption that ecosystem attributes contributing to sensitivity will shift simultaneously with chronic changes in MAP, thus reflecting the biotic and abiotic site differences found when looking across ecosystems. It is more likely that alterations of ecosystem properties will lag behind changes in precipitation (Smith et al., 2009), thus potentially causing sensitivity to shift over time. In addition, the rates of change of different sensitivity-controlling attributes will likely vary. For example, individual plant species abundances could respond within a few years (Avolio et al., 2014), while structural vegetation turnover (e.g., grassland to forest) could take decades (Habeck, 1994). Yet, we have little information about how sensitivity is individually affected by each of these drivers.

Both plant functional type and individual species abundances can modify sensitivity through differences in resource requirements, growth strategies, and resistance to drought (Fig. 1.1D). For example, CAM plants have photosynthetic machinery enabling them to persist and maintain consistent productivity levels as a system becomes very dry, yet energy costs associated with their greater water use efficiency result in slow growth rates, thus reducing sensitivity of primary productivity through maintained production in dry years and limited growth in wet years (Fig. 1.1D2). Alternately, under more mesic conditions, species with fast growth rates and low tissue maintenance costs, such as some annual grasses, may outcompete slower growing species resulting in high sensitivity. Also, species and functional groups may gain drought resistance

through morphological strategies such as deeper rooting profiles or high root to shoot ratios, allowing these species/functional groups to persist as surface soils dry out by accessing deeper soil water (Nippert and Knapp, 2007; Robertson et al., 2009). Yet, in chronically wetter conditions, they may be outcompeted by shallow rooted species or those with low root:shoot allocating less C to root structures. So, as species and functional composition in ecosystems shift to those well adapted to new levels of precipitation, the traits associated with more xeric or mesic communities tend to force sensitivity in the opposite direction of the trend seen in regional models (potentially driven by co-limitation), due to the general inherent trade-off between plant traits (e.g., high growth rates versus drought tolerance; Grime, 1977; Fig. 1.1C,D). Based on the persistence of patterns found by Huxman et al. (2004) and Sala et al. (2012) at regional scales, the impacts of co-limitation on ecosystem sensitivity likely outweigh those of species and community traits when comparing deserts to grasslands to forests. However, within a biome or over time in a single ecosystem, little is known of the relative strengths of vegetation structure versus other drivers of sensitivity.

Much of the past experimental and observational research on the sensitivity of primary productivity to altered precipitation have focused on ANPP (Knapp et al., 2002; Heisler-White et al., 2008, 2009; Muldavin et al., 2008; Fay et al., 2011; Thomey et al., 2011; Cherwin & Knapp, 2012; Sponseller et al., 2012), while many fewer have incorporated BNPP responses, despite its importance to current and future ecosystem function and services (e.g. carbon sequestration, drought resistance). Theory suggests that under alterations in soil resources, root:shoot allocations will likely shift, thus causing differential sensitivities of ANPP versus BNPP as plants allocate more biomass belowground under resource poor conditions, or aboveground for light capture under resource rich conditions (optimal allocation theory; Bloom et al., 1985). Although, this has

been shown more often with nutrient availabilities than water (Keyes and Grier, 1981; Giardina et al., 2003; Gao et al., 2011). However, findings converse to this idea have been reported in some ecosystems. For example, Frank (2007) found that, under severe drought in a northern mixed grass prairie, ANPP was insensitive while BNPP was substantially reduced, which corresponds to a reduced root:shoot under low soil moisture conditions. Also, Byrne et al. (2013) found an increase in root:shoot under low soil moisture in accordance with optimal allocation theory in a shortgrass steppe ecosystem, but found no allocation shift due to water addition in southern mixed grass prairie. So, although some ecosystem models have incorporated allocation responses to wet and dry years in their framework (e.g., Parton, 1987), predictions of C inputs (i.e., primary productivity) will be limited as long as patterns of BNPP sensitivity remain unclear.

An important service provided by ecosystems is the ability of plant growth to take up CO_2 from the atmosphere and store it in plant tissue, some of which eventually ends up in soil pools. As carbon sequestration is of particular interest in the formation of future carbon budgets, it is important to go beyond predictions of NPP responses, and examine how these changes in ANPP and BNPP will cascade to affect biogeochemical pools (Luo et al., 2014). Although primary productivity is a major avenue of carbon input to ecosystems, various other ecosystem attributes determine how much of plant carbon is incorporated into soil pools, and these attributes will likely be altered with climate change. For example, increased water availability may increase primary productivity overall, yet it may also increase microbial and soil fauna activity and thus soil respiration (Knapp et al., 1998), potentially offsetting some of the carbon gained through increased production inputs. Total soil N is important to support future plant growth, and although N inputs do not come from primary production, like C, but in the form of deposition (Goulding et al., 1998)

or N fixation (Paul, 2014), plant growth responses are important for N cycling dynamics through various plant-soil interactions (Norton and Firestone, 1991; Burke et al., 1998).

Numerous global change drivers can have large impacts on C and N cycling in ecosystems, making it important to incorporate them into assessments of biogeochemical responses to altered climate. With global change, more frequent fires are predicted in a large proportion of terrestrial ecosystems due to periodic droughts, heat waves, and anthropogenic causes (D'Antonio and Vitousek, 1992; Dale et al., 2001). In addition, fire is a management tool in many grassland systems (Knapp et al., 1998), which can have large consequences for both nitrogen and carbon in ecosystems (Tilman et al., 2000; Knicker, 2012). Indeed, ecosystem models predict substantial reductions in both C and N under increased fire frequency (Ojima et al., 1990, 1994; Schimel et al., 2001), and these losses can be expected to be dynamic if climate driven changes in water availability alter plant above/ belowground allocation of biomass. Empirical results on this subject are mixed as some have shown increases in C and N with increased fire frequencies (Chen et al., 2005; Knicker et al., 2012), while others have shown depletions (Pellegrini et al., 2014; Tilman et al., 2000). Empirical evidence for fire effects on soil C and N is quite limited since turnover of these pools typically take long periods of time, and data used to look at these trends are often complicated by factors present that may simultaneously affecting patterns of biogeochemical cycling (e.g., grazing: Perregrini et al., 2014).

In the following chapters, I examine sensitivity of ecosystem function across different grassland types as well in a single grassland over time under chronically altered precipitation regimes. I also look at the effects of these above- and belowground sensitivities on soil C and N cycling, and how they interact with a simultaneous extreme increase in fire frequency. Specifically, I address three main questions: (1) How do plant species and functional composition control

ecosystem sensitivity to altered precipitation regimes? (2) Does belowground sensitivity mirror that aboveground? And (3) What are the consequences of differential sensitivity between above- and belowground production on biogeochemical processes in the presence of annual fire regimes?

1.1 CHAPTER OVERVIEWS

In Chapter 2, I examine sensitivity of both ANPP and BNPP to increased precipitation amount and differences in storm size. I use data from an experiment I conducted in 2011 and 2012 in three US Great Plains grasslands existing across a productivity gradient. The lowest productivity site (avg. ANPP in 2011 and 2012 ~ 47.5 g m^{-2}) was a C_4-dominated shortgrass prairie located in northern Colorado at the Central Plains Experimental Range having a mean annual precipitation (MAP) of 321 mm and a mean annual temperature (MAT) of 8.6ºC. The mid-productivity site (avg. ANPP in 2011 and 2012 ~ 115.5 g m^{-2}) was a northern mixed grass prairie dominated by C_3 graminoids at the Fort Keogh Livestock and Range Research Laboratory near Miles City, eastern Montana, and receiving a MAP of 342 mm and having a MAT of 7.8 ºC. The high productivity site (avg. ANPP in 2011 and 2012 ~ 342.6 g m^{-2}) was a tallgrass prairie dominated by C_4 grasses at the Konza Prairie Biological Station (KPBS) near Manhattan in eastern Kansas, and receiving a MAP of 835 mm and having a MAT of 12.5 ºC. See Table 2.1 for more site details. At all three sites, I increased growing season precipitation by as much as 50% by augmenting natural rainfall via (1) many (11-13) small or (2) fewer (3-5) large watering events, with the latter coinciding with naturally occurring large storms. Specifically, I tested four predictions, that: (1) based on findings from regional sensitivity models (Huxman et al., 2004; Sala et al., 2012), both ANPP and BNPP responses to increased precipitation amount would vary inversely with mean annual precipitation (MAP) and site productivity, (2) functional group of vegetation at a site would influence sensitivity of the system, potentially due to physiological differences between C_3 and C_4 species, (3) increased

numbers of extreme rainfall events during high rainfall years would affect high and low MAP sites differently, and (4) responses belowground would mirror those aboveground.

In chapter 3, I explore the role that plant community composition plays in determining site-level sensitivity. I used data from two sources, both of which are long term data sets that have ANPP and precipitation data for areas experiencing very different water availabilities. I first looked at this using a long-term (20+ years) irrigation experiment, which increased precipitation by an average of 32% for two decades in a native tallgrass prairie at KPBS. This grassland represents the mesic end of the spatial gradient in the Central US, which might be expected to undergo large changes in plant composition with forecast climate change. A couple of factors about this experiment made it ideal to look for how changes in plant community structure might control sensitivity. First, after nine years of irrigation, the vegetative species composition shifted in the experiment towards a more mesic assemblage of species, but no shifts in functional type occurred. Secondly, although the experiment increased precipitation in all years, irrigation was applied on top of ambient precipitation, resulting in the maintenance of substantial year to year variability in the irrigated treatment. These two factors allowed me to examine sensitivity (Fig. 1.1B) before and after community shifts. The other way I looked at this was by comparing sensitivities between adjacent upland and lowland sites at KPBS to over 30 years of natural inter-annual variation of precipitation. These upland and lowland areas have shallow and deep soil profiles, respectively, and are host to substantially different stable plant communities.

In chapter 4, I look at how sensitivity patterns of primary productivity translate to affect biogeochemical properties of a tallgrass prairie ecosystem at KPBS, and at the interactions with another likely global change driver, increasing frequency of fire. To do this, I again used the irrigation experiment from chapter 3, although from a different area in the study. I used long-term

soil C and total N, as well as a wide suite of biotic and abiotic measurements to test the following two predictions: (1) soil C and N should reduce over time with fire, and (2) chronic irrigation would cause additional losses due to plant allocation shifts and annual volatilization of aboveground plant tissue.

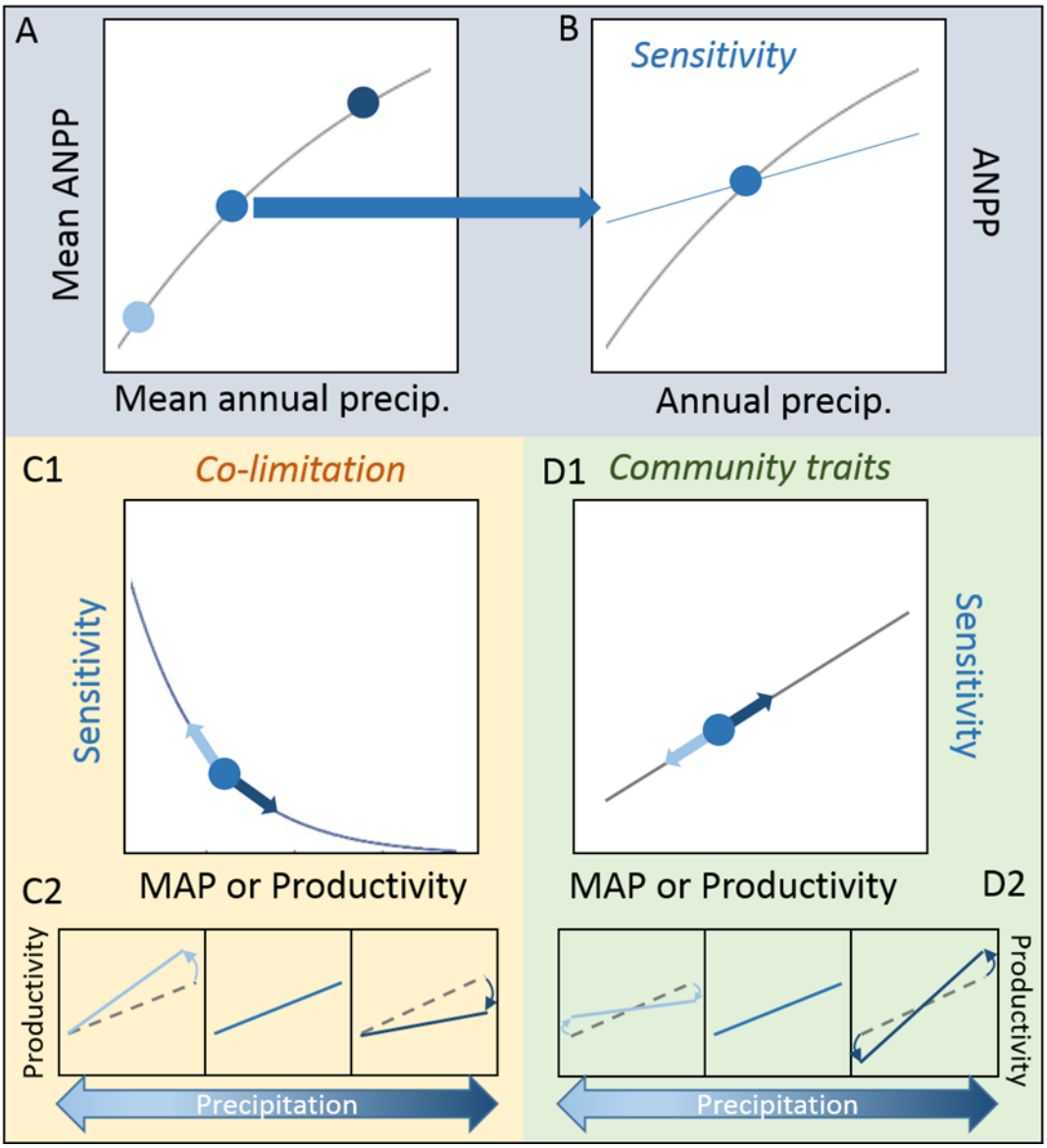

Figure 1.1. Conceptual figure showing (A) spatial and (B) temporal models of production patterns with precipitation. Ecosystems are represented by blue circles and the different shades indicate different systems along a mean annual precipitation gradient. The slope of the blue line in panel B is the relationship between annual precipitation and ANPP, but also represents the sensitivity of the system to alterations in precipitation amount. Panels C1 and D1 show how sensitivity can change across space or over time under chronically altered resource levels under two different potential mechanisms: co-limitation or community traits. Panels C2 and D2 show how these mechanisms might shift sensitivity as the system is pushed from its current state (middle panel) towards more xeric (light blue) or more mesic (dark blue) conditions.

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CHAPTER 2: CONTRASTING ABOVE- AND BELOWGROUND SENSITIVITY OF THREE GREAT PLAINS GRASSLANDS TO ALTERED RAINFALL REGIMES[1]

2.1 INTRODUCTION

Assessment of the regional-scale carbon (C) cycling consequences of forecast alterations in precipitation amount and pattern (Easterling et al., 2000; IPCC, 2007) requires knowledge of the nature and range of responses of key ecosystem processes, such as net primary productivity (NPP), across multiple ecosystems (Luo et al., 2011; Fraser et al., 2012). While forecast changes in annual precipitation amounts vary widely among climate models and geographic location (IPCC, 2007; Zhang et al., 2007), forecasts are more consistent for a general intensification of the global hydrological cycle leading to increases in inter-annual variation in precipitation amount (wetter wet and dryer dry years) and a shift in rainfall patterns towards a greater frequency of larger (IPCC, 2007) and extreme (Jentsch et al., 2007; Jentsch & Beierkuhnlein, 2008; Smith, 2011) events. Such changes have already been observed in North American grasslands; over the last 20 years in the Midwestern United States, precipitation inputs from storms 7.6 cm or larger have increased by 52% relative to long-term trends (Saunders et al., 2012). In most terrestrial ecosystems, precipitation is a major driver of C dynamics, and this is certainly true for grasslands across the central US where a strong relationship exists between mean annual precipitation (MAP) and aboveground net primary productivity (ANPP; Sala et al., 1988; Del Grosso et al., 2008). Additionally, based on regional scale analyses of long-term temporal relationships between precipitation and ANPP, productivity responses to altered precipitation amounts are expected to

[1] Wilcox, K. R., J. C. Fischer, J. M. Muscha, M. K. Petersen, and A. K. Knapp. 2015. Contrasting above-and belowground sensitivity of three Great Plains grasslands to altered rainfall regimes. Global change biology 21:335–344.

vary predictably across gradients of MAP and ANPP (Huxman et al., 2004; Guo et al., 2012). However, such inferences have been challenged by recent observational and experimental results showing a surprising degree of variability in productivity responses to altered rainfall amounts and patterns across several grassland types (Knapp et al., 2002; Frank, 2007; Heisler-White et al., 2009; Cherwin & Knapp, 2012; Byrne et al., 2013; Zhang et al., 2013a, 2013b). Much less is known about belowground net primary productivity (BNPP) responses to variations in precipitation amount (Frank, 2007; Byrne et al., 2013) and virtually all productivity responses to alterations in precipitation event size are limited to those aboveground (Knapp et al., 2002; Heisler-White et al., 2008, 2009; Muldavin et al., 2008; Fay et al., 2011; Thomey et al., 2011; Cherwin & Knapp, 2012; Sponseller et al., 2012). While information about ANPP responses is integral for predictions of changes in key ecosystem services such as forage production, BNPP measures are critical for assessments of ecosystem carbon sequestration.

Over two growing seasons, I experimentally augmented water inputs to three major central US grasslands via the addition of many small events or a few large events and quantified responses of above- and belowground productivity to increased rainfall amount and altered input pattern. I used identical protocols at all sites to alleviate concerns that divergent results from past field experiments may reflect methodological differences that can confound comparisons among ecosystems (Fraser et al., 2012). I tested predictions derived from conceptual models of production-precipitation relationships as well as inferences from recent field experiments. First, I tested the hypothesis that productivity responses to alterations in precipitation amount would vary inversely with MAP and site productivity (e.g. more arid grasslands will respond more to increased precipitation than more mesic grasslands; Huxman et al., 2004). Alternatively, more arid sites may be less responsive to wet years than mesic sites because of reduced plant (meristem) density and

low growth potential of individual plants in these ecosystems (Knapp & Smith, 2001). Second, I tested the stress threshold hypothesis (Knapp et al., 2008) which predicts that in ecosystems with low annual precipitation and high evaporative demand, a shift to fewer but larger rainfall events will have a positive impact on NPP. This is because such ecosystems are chronically in a state of water stress due to low soil moisture and large events more effectively alleviate soil water stress than smaller events. Alternatively, in higher MAP ecosystems where soil moisture is usually less limiting, many small events will maintain soil water at non-stressful levels more consistently and a shift to fewer but larger events will have a negative impact on productivity by increasing plant water stress, compared with the same amount of precipitation coming in smaller, more closely spaced events (Knapp et al., 2008). Finally, I predicted that in all three grasslands, ANPP and BNPP would respond similarly to alterations in precipitation amount and pattern, consistent with previous grassland experiments (Xu et al., 2013), but in contrast to results from forests where there is evidence that ANPP and BNPP may respond in opposing ways to changes in soil moisture (Newman et al., 2006). Determining if above- and belowground productivity respond similarly in direction and magnitude is key for predicting changes to carbon budgets under altered environmental conditions (Friedlingstein et al., 1999; Wullschleger et al., 2001).

2.2 METHODS

I examined above- and belowground vegetative responses to changes in precipitation pattern and amount in US tallgrass, northern mixed grass, and shortgrass prairies (Table 1). To incorporate natural rainfall variability into treatments, water additions occurred within the backdrop of natural rainfall patterns with amounts added based upon historical rainfall records from each site.

Experimental sites - I chose sites representative of three main ecosystem types spanning a productivity gradient within the North American grassland biome. These sites varied in their climatic regimes, soil properties, and composition of vegetation (Table 2.1), spanning many of the key gradients well-documented across the central US grassland region.

The shortgrass prairie (SGP) site was located in Northern Colorado at the Central Plains Experimental Range in an area that had been protected from cattle grazing for 12 years at the start of the experiment. This site receives, on average, 321 mm of rainfall annually, much of which falls during the growing season (May – August), and has a mean annual temperature (MAT) of 8.6°C (Lauenroth & Burke, 2008). ANPP in control plots during 2011 and 2012 was 47.5 g/m^2 and vegetation is dominated by perennial, rhizomatous C_4 grasses, particularly *Bouteloua gracilis*. The northern mixed grass prairie (NMP) site was located in Eastern Montana at the Fort Keogh Livestock and Range Research Laboratory in an area ungrazed since 1999. This site receives only slightly more precipitation annually (342 mm) than SGP, but MAT is lower (7.8°C; 1960-2010 USCRN data; Diamond et al., 2013) and the region is more productive (ANPP from control plots 115.5 g/m^2). This site is dominated by perennial C_3 graminoids – primarily *Hesperostipa comata*, *Pascopyrum smithii*, and *Carex filifolia*. The tallgrass prairie (TGP) site was located in the Flint Hills region in Eastern Kansas at the Konza Prairie Biological Station in the upland portion of a watershed ungrazed for over 30 years. In contrast to the other two sites, this site was burned in each year of this study and historically has been burned frequently, reflecting historical and managed fire regimes for the region (Knapp, 1998). The TGP site receives an average of 835 mm of rainfall annually. ANPP in control plots was 342.6 g/m^2, and consisted mostly of perennial, rhizomatous, C_4 grasses – namely *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium* (See Table 2.1 for additional information about each site).

Experimental treatments – I added water to the experimental plots in two different patterns while keeping total rainfall amount constant between treatments. I added either numerous (11-13) small events spaced relatively evenly throughout the growing season (Many-Small treatment) or larger amounts of water were added to naturally occurring large storms a few times (3-5) over the course of the growing season (Few-Large treatment). Control plots received ambient precipitation (with one exception – see *Treatment effects on precipitation regimes* below) which permitted me to assess the effects of increases in total precipitation as well as alterations in event size and number. The treatments were applied based on three criteria: (1) If no natural large rain event (see paragraph below for "large" event size categorization details) occurred in a seven day period, a small water addition was applied to the Many-Small treatment, (2) when a natural large precipitation event occurred, the sum of all water previously added to the Many-Small treatment since the last large event was then added to the Few-Large treatment, and (3) if there were no large precipitation events for 28 consecutive days, a water application was added to the Few-Large treatment.

Natural precipitation regimes vary substantially among these three grasslands so I based the size of the small water additions and the timing of large events on simulations of different combinations of these two variables using historical data from each site. The goal of these simulations was to identify treatment regimes that would consistently manipulate precipitation pattern and amount among the three sites while maintaining total precipitation amounts within historical ranges of variability. Based on our simulations, I added 5.6 mm of water every 7 days for the Many-Small treatment at the SGS and NMP grasslands and 10.3 mm at TGP. I designated "large" rainfall events (i.e. events that triggered the additions to the Few-Large treatment) as those

of a size greater than or equal to: 9.9 mm (85th percentile event size) at SGP, 9.1 mm (85th percentile) at NMP, and 19.8 mm (80th percentile) at TGP.

Treatments (local aquifer water) were applied with a garden watering wand in the morning or evening to minimize evaporative loss during watering events. Large event additions were applied as 5-10 mm portions separated by ca. 5 minutes to allow water to penetrate into the soil and avoid aboveground lateral flow.

Treatment effects on precipitation regimes – From late May through August of 2011 and 2012 at each site, precipitation was manipulated so that total growing season (May-August) rainfall was increased 15-50% in the Many-Small and Few-Large treatments relative to control plots. For both years, this precipitation increase required 11-13 events in the Many-Small treatment and 3-5 events in the Few-Large treatment (Fig. 2.1). The size of added events across sites and the two years ranged from 5.6-10.3 mm in the Many-Small treatment and from 12.3-37.8 mm (added on top of large ambient storms) in the Few-Large treatment (Table A1-1). The mean size of rainfall events, the proportion of precipitation from large events (defined as precipitation events in the 80th percentile), the number of and proportion of rainfall from extreme events (95th percentile), and the average length of dry periods were all increased in the Few-Large treatment relative to the Many-Small treatment in both years and at all sites while the number of events was decreased (Table A1-1). All Few-Large events (i.e. the sum of ambient and added rainfall during a treatment application) fell within the natural range of large rainfall events at each site such that, (1) treatment events were never larger than the long-term maxima and (2) the average size of treatment events were similar to the long-term mean of large event sizes (Table A1-1). In 2011, control plots received ambient precipitation, but due to low levels of growing season precipitation at all sites in 2012, one water addition corresponding to the 90th percentile event size at each site (SGP: 15.7 mm; NMP: 15.6

mm; TGP: 37.4 mm) was added to all plots when the cumulative growing season precipitation dropped below the historical 25th percentile.

Experimental design – At each site, ten 25 m^2 (5 x 5 m) blocks were established as a randomized complete block design in a relatively flat area with plant communities representative of the larger area. Within these, 4 m^2 (2 x 2 m) subplots (two watering pattern treatments, one control, and one empty) were randomly assigned with 0.5 m between subplots. In the center of each subplot, 1.96 m^2 (1.4 x 1.4 m) sampling plots were established with a 0.8 m buffer between the edge of sampling plots and adjacent treatment subplots. Soil moisture measurements indicated that this buffer was sufficient to avoid any influence of adjacent water applications. Due to inherently low levels of green biomass in SGP, mesh wire fencing (1 m tall) was installed around each block to minimize small mammal herbivory in watered plots.

Data collection – Throughout the 2011 and 2012 growing seasons (May-Sept), hourly measurements of volumetric soil water content integrated over 0-20 cm were made at each site (ECH_2O probes, Decagon Devices Inc., Pullman, WA, USA) and averaged to obtain daily means in three blocks at each site. Probes were calibrated using soil bulk density values and gravimetric soil moisture measurements over a range of soil moisture conditions.

Site community composition at each site was assessed by estimating plant species abundances visually to the nearest 1% in a 1m^2 area within each control plot in 2011 and 2012.

Aboveground net primary productivity (ANPP) of herbaceous vegetation was estimated at each site by harvesting all aboveground biomass at the end of the growing season (September) in 3, 0.1 m^2 subplots per sampling plot in 2011 and 2, 0.1 m^2 subplots per sampling plot in 2012. Samples were dried at 60°C for 48 hours, sorted to remove any previous year's plant material, and weighed.

Belowground net primary productivity (BNPP) was estimated using root ingrowth cores (Persson et al., 1980) in one subplot in 2011 and two subplots in 2012 (the latter were pooled) at each site. Mesh cylinders 5 cm in diameter made from 2 mm fiberglass screen were inserted 30 cm deep into the ground in May to sample the majority of root growth (Jackson et al., 1996). These cores were filled with native soil sieved with a 2 mm screen to remove preexisting root biomass, and then packed to a density approximate of natural soil conditions. Root ingrowth cores were removed in September and separated into 0-15 ($BNPP_{0-15}$) and 15-30 cm ($BNPP_{15-30}$) depths. Roots were removed from the soil using a hydropneumatic root elutriator (Smucker et al., 1982) for SGP and NMP sites and by hand washing for the TGP site (due to high soil clay content). Roots were dried at 60°C for 48 hours, and weighed. Ash mass of samples was obtained by heating samples in a muffle furnace at 450°C for four hours and then subtracted from ash-inclusive dry mass. ANPP and BNPP estimates for each plot were summed to calculate total NPP per plot.

Statistical analyses – Soil moisture measurements for each site and treatment were compared over the entire growing season using repeated-measures ANOVA with an autoregressive heterogeneous covariance structure (proc MIXED in SAS, Version 9.3, Cary, NC, USA). Least squared means were compared among treatments when the site-based model showed the treatments had a significant overall effect. The response variables ANPP, BNPP, NPP, BNPP:ANPP ratio, and $BNPP_{0-15}$:$BNPP_{15-30}$ ratio were natural log transformed to satisfy normality assumptions and analyzed using repeated-measures ANOVA with heterogeneous compound symmetry covariance structure over both years of the experiment (MIXED procedure in SAS). Years were combined in a repeated measures ANOVA because of non-significant interactions between treatment and year (Table A2-3), different variances between the two years, and a lower corrected Akaike information criterion (AICc) in the repeated measures model allowing for

different variances between years than the model keeping the variances constant. To assess differences between ANPP and BNPP sensitivity within a site, I calculated differences between watering treatment and control productivity (for both ANPP and BNPP) pairing plots within a block and then divided this by the amount of precipitation which treatment plots received throughout the growing season. I then analyzed these sensitivity values using a repeated measures ANOVA with heterogeneous compound symmetry covariance structure over both years of the experiment. Differences in above- and belowground sensitivity to watering pattern were assessed by comparing ANPP and BNPP responses in each treatment to control plots (i.e. did the treatments cause a significant response?).

2.3 RESULTS

Soil moisture responses – Soil moisture was measured in both years at all three sites, but I report only the 2012 data set due to two several week periods of probe malfunctions at two of the sites in 2011. For periods of data overlap between the two years, 2011 responses to treatments were consistent with 2012 data, as expected given that treatments were applied with the same protocol each year. In 2012, growing season average soil moisture levels in control plots were significantly different among sites (Table A2-1, Fig. 2.2). At all sites, small and large water additions resulted in increased soil moisture (Fig. 2.2), but despite obvious differences among control and treatment plots in soil moisture after water additions, season-long soil moisture averages were not significantly different among treatments in SGP or TGP (Table A2-1). Conversely, both patterns of water addition treatments led to significantly higher average soil moisture levels at NMP (Table A2-1).

Productivity – Treatment effects on all direct productivity measures varied by site (i.e. significant Site*Treatment interactions; Table A2-2) so sites were examined independently. I show

productivity responses in three ways: (1) as the response to watering pattern treatments relative to the control (Fig. 2.3a-c), (2) as the absolute response to watering treatments regardless of watering pattern (i.e. Many-Small and Few-Large treatments were pooled) relative to the control (Fig. 2.3d-f), and (3) as the productivity response to water addition standardized by the amount of precipitation added in a particular site/year relative to the control (Huxman et al., 2004; Fig. 2.3d-f insets). Precipitation additions significantly increased ANPP, BNPP, and Total NPP in both TGP and SGP, but had no effect in NMP (Fig. 2.3, Table A2-3). In TGP, both the Many-Small and Few-Large treatments led to significant increases of ANPP, but there was no difference between the watering pattern treatments (Fig. 2.3a, Table A2-4). Conversely, BNPP in TGP was significantly higher than in the control only in the Few-Large treatment (Fig. 2.3b). Regardless of watering pattern at the TGP site, water addition increased ANPP and BNPP by 47.2 +/- 23.6 g/m^2 (μ +/- s.e.) and 40.0 +/- 11.8 g/m^2, respectively which corresponded to 13.8 and 22.6% increases (Fig. 2.3d, e). In SGP, both the Few-Large and Many-Small treatments increased ANPP relative to the control and ANPP in the Few-Large treatment was higher than in the Many-Small treatment (Fig. 2.3a, Table A2-4). BNPP in the Many-Small and Few-Large treatments in SGP was significantly higher than in the control, but there was no effect of event size/number (Fig. 2.3b, Table A2-4). Regardless of watering pattern, water addition led to a 14.0 +/- 3.9 g/m^2 and 58.6 +/- 6.6 g/m^2 increase in ANPP and BNPP (Fig. 2.3d, e), respectively or 29.4 and 102.0% increases relative to the control at SGP (Fig. 2.3d, e). In SGP and TGP, total NPP in the Many-Small and Few-Large treatments were significantly higher than the control, yet there was no significant difference between the two treatments. Overall, water addition caused a 72.6 +/- 8.6 g/m^2 increase in total NPP in SGP and a 75.28 +/- 40.3 g/m^2 increase in TGP (Fig. 2.3f) corresponding to 69.1 and 14.5% increases, respectively (Fig. 2.3f).

I compared sensitivity of different productivity types (i.e. ANPP and BNPP) and found that the relationship between ANPP and BNPP sensitivity differed significantly across sites (Table A2-5) so I analyzed sensitivity individually at each site. In TGP and NMP, ANPP and BNPP sensitivities were not significantly different from each other while in SGP, BNPP sensitivity was almost fourfold greater than that of ANPP (Fig. 2.3d, e insets; Table A2-5).

The ratio of belowground to aboveground net primary productivity (BNPP:ANPP) varied significantly among sites with the highest ratio in SGP (1.78 +/- 0.18), followed by NMP (1.34 +/- 0.11), and TGP (0.55 +/- 0.02). Neither precipitation pattern nor precipitation amount affected BNPP:ANPP and treatment effects did not vary significantly by site ($F = 1.79$, $P = 0.14$, Fig. A2-2).

Finally, I tested for differences between BNPP at 0-15 and 15-30 cm depths. At all sites, $BNPP_{0\text{-}15}$ was higher than $BNPP_{15\text{-}30}$ (Fig. 2.4; Table A2-1), but the mean ratio of $BNPP_{0\text{-}15}$: $BNPP_{15\text{-}30}$ differed among sites ($F = 4.25$, $P = 0.02$). The ratio in NMP was significantly lower than both SGP (46.8% reduction; $t = 2.66$, $P = 0.01$) and TGP (44.2% reduction; $t = 2.35$, $P = 0.03$) while the ratios did not significantly differ between SGP and TGP ($t = 0.26$, $P = 0.80$). I found no significant treatment effects at any site concerning the distribution of BNPP in the soil.

2.4 DISCUSSION

There is now abundant experimental evidence that forecast alterations in precipitation event size and number, in addition to amount, will likely affect C cycling processes in terrestrial ecosystems (Knapp et al., 2002; Heisler-White et al., 2008, 2009; Chen et al., 2009; Hao et al., 2013; Kulmatiski & Beard, 2013; Zhang et al., 2013a, 2013b). Indirect evidence is also emerging that increases in event size may interact with drought, muting reductions in productivity in water-limited ecosystems (Cherwin & Knapp, 2012; Raz-Yaseef et al., 2012). Here I extend this body of

research by assessing the impact of altered event size and number during years with above average precipitation. Unlike the studies above, I also measured BNPP, which is especially important in grasslands where BNPP often exceeds ANPP (Weaver, 1954; Sims & Singh, 1978; Milchunas & Lauenroth, 2001). I conducted identical experiments in shortgrass, northern mixed grass, and tallgrass prairie sites in the central US to test three hypotheses: (1) that both ANPP and BNPP sensitivities to increased precipitation amount would vary inversely with MAP (Huxman et al., 2004), (2) that increased event size would affect high and low MAP sites differently (Knapp et al., 2008), and (3) that belowground responses to increases in precipitation would be consistent with aboveground responses.

Responses to increases in precipitation – Huxman et al. (2004) estimated sensitivity of ANPP to changes in precipitation based on slopes of production-precipitation relationships in sites spanning a wide range of MAP. When looking at ANPP responses to water additions that were proportional to each site's average rainfall (ca. 30%) in both of the C_4 dominated grasslands, I found that although ANPP in the most productive site with the highest MAP (TGP) responded the most to increases in precipitation and the driest site (SGP) responded the least (Fig. 2.3d), this response pattern was reversed for BNPP (Fig. 2.3e) resulting is no absolute difference between these two sites in the response of total NPP to increased precipitation (Fig. 2.3f). When responses were expressed as sensitivity (change in productivity/ unit change in precipitation; Huxman et al., 2004; Fig. 2.3 insets), contrary to the general trend reported by Huxman et al. (2004), sensitivity of ANPP was greatest in TGP (highest MAP) and lower in SGP. This pattern is consistent with the meristem limitation hypothesis which predicts that more arid low productivity ecosystems have limited capacity to respond to increases in precipitation due to existing traits of resident species (Lavorel & Garnier, 2002) and the inherent tradeoff between drought tolerance and growth

potential (Chapin, 1980). However, our findings that BNPP and NPP sensitivities to increased precipitation were greater in SGP (Fig. 2.3e, f insets) do provide support for the Huxman et al. (2004) model of sensitivity to alterations in precipitation.

In contrast to the SGP and TGP, the lack of sensitivity of productivity (ANPP, BNPP and NPP) at NMP (intermediate productivity and MAP) to added growing season precipitation and altered soil moisture levels (Fig. 2.2), suggests that northern mixed grasslands are relatively insensitive to wet growing seasons as well as droughts (Heitschmidt et al., 1999; Frank, 2007; White et al., 2014). Although co-limiting resources can control productivity when one resource is overly abundant (Tilman, 1982) as in NMP in 2011 (Fig. 2.1), the lack of evidence of greater nitrogen limitation in NMP relative to other sites (Dodd & Lauenroth, 1979; Haferkamp et al., 1993; Collins et al., 1998) and an identical response during relatively low ambient precipitation inputs and soil moisture levels in 2012 (Fig. 2.2b) lead us to suggest that co-limitation by nitrogen is not the primary factor controlling the minimal response in NMP. Instead, I posit that the lack of sensitivity to growing season precipitation inputs reflects the early season growth dynamics of this C_3 dominated system (Table 2.1; Ehleringer, 1978; Pearcy et al., 1981; Vermeire et al., 2008, 2009) as well as much greater reliance on soil moisture inputs from winter and early spring precipitation (Vermeire et al., 2008), including snowmelt. Indeed, our results showing that root production in NMP tended to occur more evenly throughout the upper 30 cm of the soil relative to the other two grasslands (Fig. 2.4) are consistent with regional rooting depth patterns (Schenk & Jackson, 2002) and the notion that NMP relies less on summer rains (which tend to wet soil layers closer to the surface) than the more shallowly rooted SGP and TGP. Only when early-season moisture inputs are low has BNPP been shown to decline in these grasslands (Frank, 2007). Overall, the lack of response of this grassland to the precipitation treatments imposed (both amount and pattern; Fig.

2.3) suggests that this widespread grassland type is likely to respond uniquely – relative to the C_4 grasslands of the central and southern US – to climatic changes that occur during the summer.

Responses to altered precipitation patterns – In contrast to NMP, both TGP and SGP responded to watering pattern, but in opposing ways above- and belowground (Fig. 2.3a, b). A shift from the Many-Small to the Few-Large precipitation pattern had no effect on ANPP in TGP, contrary to previous studies in this grassland (Knapp et al., 2002; Heisler-White et al., 2009; Fay et al., 2011), whereas the Few-Large watering pattern significantly increased ANPP in SGP, as predicted by Knapp et al. (2008) and confirmed by several other studies (Heisler-White et al., 2009; Thomey et al., 2011; Sponseller et al., 2012). Watering pattern had less impact belowground for SGP yet more for TGP. These incongruent effects above- and belowground resulted in a lack of sensitivity of NPP to alterations in precipitation pattern in both grasslands (Fig. 2.3a-c).

Are BNPP responses to changing precipitation regimes consistent with ANPP? Across these three grassland types, responses of ANPP and BNPP were not consistent with regards to changes in precipitation amount and pattern. In SGP, the differential sensitivities of ANPP and BNPP to precipitation amount contrasted with the similar ANPP and BNPP sensitivities in TGP (Fig. 2.4d-f insets). In NMP, there were no differences between responses of ANPP and BNPP as both were insensitive to changes in precipitation regimes. Although other studies have shown discordant responses of BNPP and ANPP to reductions in precipitation (Frank, 2007; Byrne et al., 2013), most sensitivity theory is based on ANPP (Knapp & Smith, 2001; Huxman et al., 2004; Knapp et al., 2008) not BNPP. This pattern of above- and belowground sensitivities across the two C_4 dominated sites suggests that increases in rainfall may impact the ecosystem service, forage production, more in the higher rainfall regions of the central US, whereas total vegetative biomass

inputs (potentially affecting carbon sequestration rates) will be more responsive to precipitation inputs in more arid regions.

As annual precipitation amounts and patterns are altered via global change, predictions of ecosystem responses are needed to help inform policy and land management decisions. I show here that ecosystems within a single biome can vary greatly in their responses (ANPP, BNPP and NPP) to increases in precipitation amount and altered pattern. Although several predictions of ecosystem sensitivity or resistance to climate change have been based on gradients in resource levels (Huxman et al., 2004; Cleland et al., 2013) or the inherent productivity of the ecosystem (Grime et al., 2008; Hudson & Henry, 2010), the unique lack of response to either increased precipitation amount or altered pattern in the C_3 dominated NMP suggests that other ecosystem attributes such as vegetative functional composition (Table 2.1), root depth distribution (Fig. 2.4) and the timing of precipitation inputs may be important in modifying ecosystem sensitivity to an intensification of the hydrological cycle.

2 TABLES

Table 2.1. Climate, soil, and vegetative characteristics of the Central Plains Experimental Range, Nunn, CO (SGP), Fort Keogh Livestock and Range Research Laboratory, Miles City, MT (NMP), and Konza Prairie Biological Station, Manhattan, KS (TGP). All vegetation characteristics except mean ANPP were calculated from species compositional measurements taken in $1m^2$ control plots in 2011 and 2012. ANPP values reflect average plot level measurements in control plots over the two years of the experiment.

		SGP	NMP	TGP
General	Latitude	40°84'N	46°31'N	39°09'N
	Longitude	104°76'W	105°98'W	96°55'W
	Grassland type	Semiarid shortgrass	Northern mixed grass	Mesic tallgrass
Climate	MAP (mm)*	321	342	835
	Mean growing season precipitation (mm)*	204	193	428
	MAT (°C)*	8.4	7.8	12.5
Soil	A horizon texture**	Fine sandy loam	Loam	Silty clay loam
	B horizon texture**	Sandy clay loam	Clay Loam	Silty clay loam
	Pedon description**	Aridic Argiustoll	Aridic Argiustoll	Udic argiustoll
	Available water capacity**	Moderate -17.5 cm	High – 28.7 cm	Moderate – 16.3 cm
Vegetation	Mean ANPP (g/m^2)	47.5	115.5	342.6
	Species pool***	35	36	38
	Species richness (S)	6.4	13.4	9.5
	Diversity (H')	0.97	1.72	1.30
	Evenness	0.54	0.67	0.58
	C3 grass (%)	20.5	83.6	13.2
	C4 grass (%)	70.7	3.1	81.0
	Forb (%)	5.4	8.9	3.0
	Annual (%)	2.5	13.5	0
	Perennial (%)	96.5	86.4	100

* Obtained from NOAA climate data from Miles City, MT, Nunn, CO, and Manhattan, KS.
** Soil Survey Staff (2013)
***Total number of species encountered in all control plots within a site

2 FIGURES

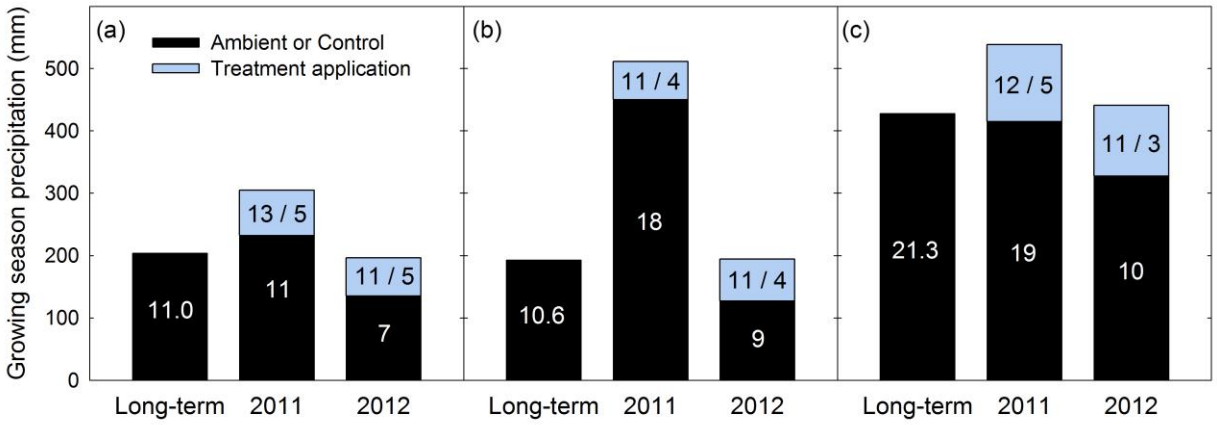

Figure 2.1. Long-term and treatment growing season (May – August) precipitation characteristics at all sites – **(a)** Central Plains Experimental Range (SGP; 1969-2010), **(b)** Fort Keogh Livestock Range and Laboratory (NMP; 1960-2010), and **(c)** Konza Prairie Biological Station (TGP; 1960-2010). Numbers within the black bars indicate the average number of events greater than 5 mm in historical records in the Long-term bars or the number of events greater than 5 mm experienced by the control plots in the 2011 and 2012 bars. The first number within the lightly shaded or blue bars indicates the number of water additions added to the Many-Small treatment and the second indicates the number added to the Few-Large treatment.

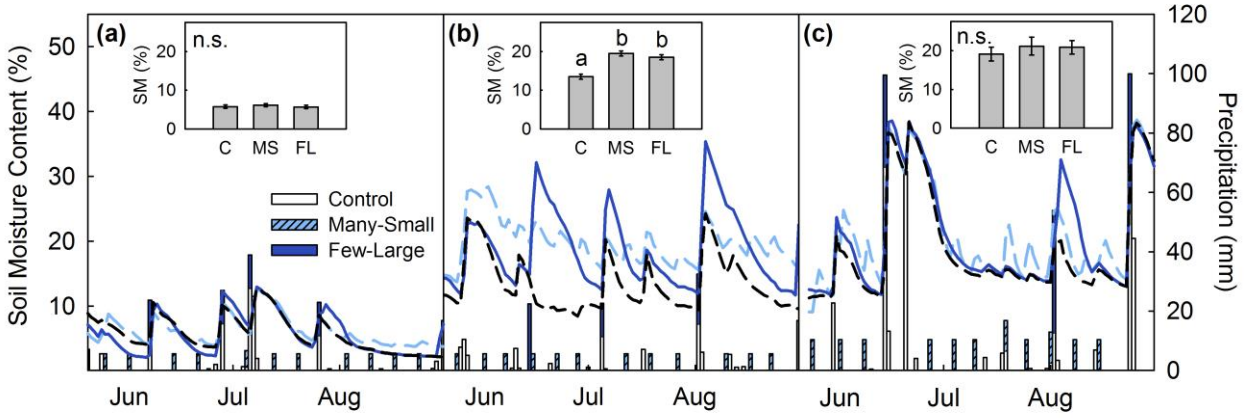

Figure 2.2. Daily soil moisture and precipitation measurements during the 2012 growing season for all treatments – Many Small (light, dashed lines and light, hashed bars), Few-Large (dark, solid lines and bars), and Control (black dashed lines and unfilled bars) – at the **(a)** Central Plains Experimental Range (SGP), **(b)** Fort Keogh Livestock and Range Laboratory (NMP), and **(c)** Konza Prairie Biological Station (TGP). Insets: Growing season averages (May 23 – August 31, 2012) of soil moisture in Control (C), Many-Small (MS), and Few-Large (FL) treatments. Different letters represent significant differences of least squared means between treatments within a site. P values were adjusted for multi-comparisons using Tukey honest significant difference method.

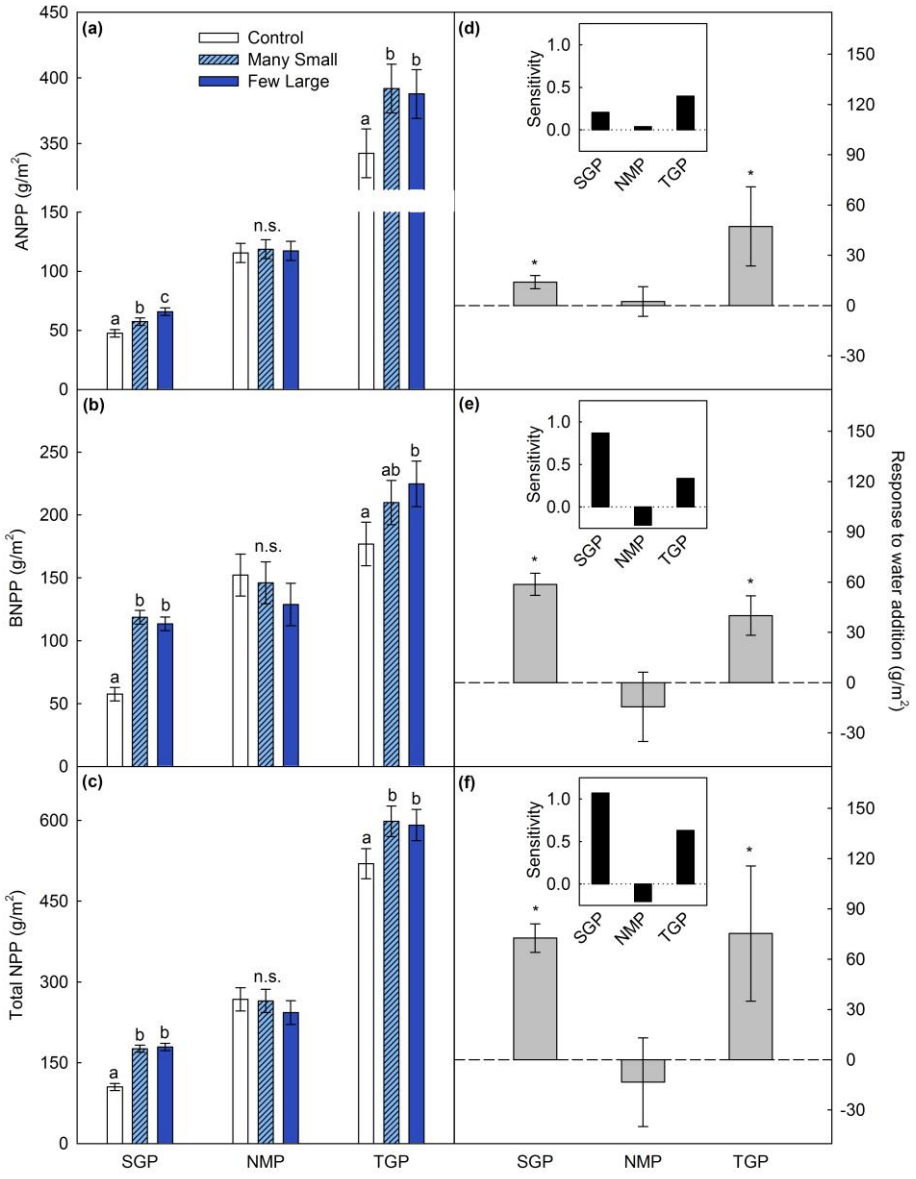

Figure 2.3. Productivity responses to altered precipitation regimes at all sites – Central Plains Experimental Range (SGP), Fort Keogh Livestock and Range Laboratory (NMP), and Konza Prairie Biological Station (TGP). Responses are organized into those resulting from water added in different patterns **(a - c)** and overall response to water addition regardless of pattern **(d – f).** Productivity is partitioned into aboveground **(a, d)**, belowground **(b, e)**, and total **(c, f)** categories. Different letters indicate a significant difference based on multi-comparison of least squared means. Asterisks in panels d – f indicate that responses due to water addition are significantly different than control plots (dashed line) at the $\alpha = 0.05$ level. Insets: Sensitivity calculated as the change in productivity (g/m^2) per unit change in precipitation (mm) in pooled water addition treatments relative to control plots at each site.

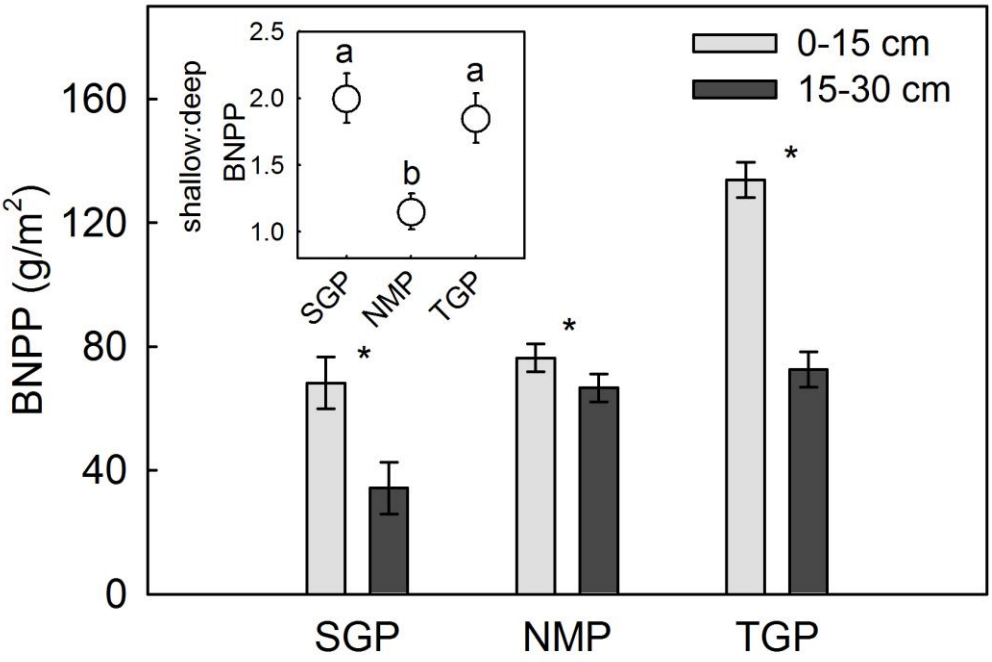

Figure 2.4. Belowground net primary productivity in 0-15 cm and 15-30 cm soil layers at all three sites – the Central Plains Experimental Range (SGP), Fort Keogh Livestock and Range Research Laboratory (NMP), and Konza Prairie Biological Station (TGP). Because there was no treatment effect on rooting depth, values shown are averaged over treatments at each site. Asterisks denote significant differences ($\alpha = 0.05$) between rooting depths within a site. Inset: Ratio of shallow (0-15 cm) to deep (15-30 cm) BNPP for each site. Data are presented in the original scale, but analyses used log-transformed values to meet normality assumptions for analysis of variance. Different letters denote significant differences between rooting depth ratios at different sites.

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CHAPTER 3: WILL CHANGES IN WATER AVAILABILITY ALTER ECOSYSTEM SENSITIVITY TO PRECIPITATION? TESTING PREDICTIONS FROM REGIONAL MODELS AT A LOCAL SCALE

3.1 INTRODUCTION

Global climate models forecast both increases and decreases in mean annual precipitation depending on geographic location (IPCC, 2013, Zhang et al., 2007). When combined with alterations in other modifiers of ecosystem water balance (increased atmospheric CO_2, warmer air temperatures, altered humidity), a substantial proportion of terrestrial ecosystems are expected to become either drier or wetter, with recent analyses confirming this forecast (Greve et al., 2014). A more consistent prediction of climate models is an increase in inter-annual precipitation variability forecast for all terrestrial ecosystems (IPCC, 2013). This latter prediction is important because precipitation is a major driver of terrestrial aboveground net primary productivity (ANPP) over time (i.e., in response to inter-annual rainfall variation within an ecosystem) as well as at regional ($>10^3$ km) to continental spatial scales (i.e., across ecosystems with different mean annual precipitation amounts; Sala et al., 1988, 2012, Huxman et al., 2004, Del Grosso et al., 2008). Indeed, the functional relationship between precipitation and ANPP both temporally and spatially is central to understanding the dynamics of Earth's carbon cycle.

A key difference between temporal (within-system) and spatial (across-system) relationships is that plant community composition often remains relatively constant in temporal models, but varies dramatically over regional gradients. As a result, in addition to precipitation amount, the attributes of more xeric versus more mesic plant communities determine regional-scale responses to inter-annual variation in precipitation (Lauenroth and Sala, 1992; Lavorel and Garnier, 2002). Spatial and temporal models describing ANPP versus precipitation relationships

have been linked by observations that the temporal sensitivity of ANPP to precipitation variability (response in ANPP/mm change in precipitation: $ANPP_{sensitivity}$) varies inversely with MAP and ANPP at regional to continental scales (Huxman et al. 2004, Sala et al. 2012, Golodets et al., 2013). Thus, as MAP increases across large spatial gradients, plant communities shift from those dominated by xeric (less productive, shorter statured) species to more mesic (more productive, taller) species and ANPP increases (Sala et al., 1988), yet the temporal responsiveness of ANPP to wet and dry years decreases (Huxman et al., 2004). As a consequence of this pattern, ecosystems that become chronically wetter with climate change would be predicted to become more productive, develop plant communities with more mesic species and display lower temporal $ANPP_{sensitivity}$, with the opposite predictions made for ecosystems that become drier.

I assessed how well regional models relating patterns of MAP, ANPP, plant community composition and $ANPP_{sensitivity}$ predict responses within an ecosystem subjected to differences in water availability that have elicited plant community change. I used two long-term (> 20 year) data sets – one experimental and one observational – that directly linked altered water availability and responses in plant community composition to expected changes in the temporal sensitivity of ANPP to precipitation variability. With the experimental data set I was able to assess productivity responses and shifts in $ANPP_{sensitivity}$ to a chronic increase in water availability both in the short-term (before community change occurred) as well as after community change had taken place. Whereas with the observational data set, I assessed productivity and $ANPP_{sensitivity}$ in relatively stable plant communities that reflected long-term differences in water availability. I tested a prediction from regional models (Huxman et al., 2004, Sala et al., 2012) that with chronic increases in water availability and concurrent plant community change, $ANPP_{sensitivity}$ would be reduced in this grassland. With the observational data set, I predicted that within an ecosystem, sites with

reduced water availability and ANPP, but greater abundances of more xeric plant species would have increased $ANPP_{sensitivity}$ than wetter sites with higher ANPP and more mesic plant communities. This expectation is also consistent with patterns seen at regional scales (Huxman et al., 2004; Sala et al., 2012).

3.1 METHODS

Study Sites – I utilized long-term ANPP, plant species composition, and daily precipitation data from the Konza Prairie Biological Station (KPBS). KPBS is a native tallgrass prairie ecosystem that receives an average of 834 mm of precipitation annually, most of which falls during the growing season (April-September; Hayden, 1998), has a mean annual temperature of 12.5 °C (USCRN data; Diamond et al., 2013), and a mean ANPP in productive lowland sites of ~528 g m^{-2} (Knapp et al., 1998). Vegetation at the site is dominated by a few rhizomatous C_4 perennial grass species, namely *Andropogon gerardii* and *Sorghastrum nutans*, but also species found more commonly in wetter ecosystems to the east (e.g., *Panicum virgatum*, *Tripsacum datyloides*) and drier grasslands to the west and south (e.g., *Schizachyrium scoparium*, *Bouteloua curtipendula)* can be found throughout the site (Towne, 2002).

Data sets – I examined two data sets from KPBS – consisting of ANPP, plant species composition, and precipitation measurements – representing chronically altered soil water availability. The first data set was from the Irrigation Transect Experiment (IrrT), where plots (n=9; simple spatial pseudo-replication (Hurlbert, 1984) was accounted for using transect as a random effect within mixed effects models, see Millar and Anderson, 2004 and Lazic, 2010) were irrigated from 1991-2011 (average of 256 mm total added annually on top of ambient rainfall) May through September to remove water limitation during the growing season (see Collins et al., 2012 and Appendix III for more information on the experimental design). The second data set

(upland-lowland comparison – ULC) encompassed 50 m transects (n=4) located in upland areas with shallow soils (~20 cm) and adjacent lowland areas with deep soils (~50 cm; Schimel et al., 1991; n=4 transects; 1D watershed in the PAB01 data set from the Konza Prairie Long Term Ecological Research station). Both datasets were collected from annually burned sites (23 years for IrrT with fire events every ~ 3 years previous to that, and 30+ years for ULC) that were ungrazed for more than 40 years. Fire is historically important in this grassland for its origin and maintenance (Axelrod, 1985), and frequent fire is a management tool today (Briggs & Gibson, 1992).

ANPP Measurements – Estimates of aboveground net primary productivity (ANPP) were obtained in IrrT from 1991-2011 by clipping all aboveground live plant biomass to ground level in six 0.1 m^2 subplots per plot and in five 0.1 m^2 subplots per transect in ULC (1983-2011) yearly in late August - early October. Biomass was dried for 48 hours at 60° C, sorted to major functional type (e.g., graminoid, forb, woody), and weighed. Similar trends were found when including or excluding woody biomass measurements so all reported analyses use ANPP excluding woody biomass due to increased variability coinciding with its inclusion. Measurements from subplots were averaged across each plot in IrrT and averaged across each transect in ULC.

Plant Species Composition – Plant community composition was measured by visually estimating aerial cover of each species using a modified Daubenmire cover scale (Daubenmire, 1959, Abrams & Hulbert, 1987). This was done once per year in July for IrrT and twice per year in May-June and August-September for ULC. Aerial cover was sampled within permanent 10 m^2 circular plots for: watered and control plots in IrrT (n = 9 for each treatment), and upland and lowland plots in ULC (n = 20 for each topographic position). For analysis, cover classes were converted to the midpoint of the cover range, max covers for each species in each year between

early and late season sampling were used, and relative covers for each species within a plot were calculated by dividing each species' cover by the summed covers among all species in the plot.

Statistical Analyses – I assessed differences in plant community composition between treatments in IrrT and topographic position in ULC in each year by testing for differences between centroid locations using 999 permutational MANOVA (Anderson, 2001) with a Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957). I determined which species were most important in driving differences between treatments or topographic positions by pooling community data for all years where communities were significantly different ($\alpha = 0.05$) and conducting similarity percentages analyses (SIMPER). Plant compositional analyses were conducted using PRIMER v6 (Plymouth, UK).

I used repeated measures mixed models (Proc MIXED, SAS v9.3, Cary, NC, USA) with autoregressive covariance structure, based on corrected AIC comparisons, to look for differences in relative cover of the five species which most contributed to differences of community centroids between treatments or topographic position. Additionally, relative covers of functional groups were calculated by summing relative covers of all species within a functional group and analyzed using a repeated measures mixed model with autoregressive covariance structure. Cover values were logit transformed as necessary to satisfy normality assumptions.

I compared productivity responses across data sets and treatments/ topographic position using a repeated measures ANOVA, with years as the repeated variable, and a compound symmetry covariance matrix, again based on corrected AIC comparisons. Productivity responses between time periods in IrrT were compared with a repeated measures ANOVA and Satterthwaite approximations of standard errors were incorporated to account for different lengths of time and variance making up the two periods.

I first assessed and then compared $ANPP_{sensitivity}$ – defined as the slope of the relationship between inter-annual growing season precipitation and ANPP using linearized regressions (incorporating transect as a random effect in IrrT) – for each treatment/topographic location within each data set. ANPP was log-transformed as necessary to satisfy assumptions of normality. Differences between sensitivities were determined in one of two ways: (1) if one relationship was significant and another was not, sensitivities were determined to be different; (2) if both slopes were significant, sensitivity was determined to be different in the case of a significant ($\alpha = 0.05$) interaction between treatment (or topographic position) and growing season precipitation.

3.2 RESULTS

I initially assessed productivity responses collectively for irrigated vs. non-irrigated (i.e., ambient) plots and between upland and lowland topographic areas. I found that total and graminoid ANPP were both greater in irrigated and lowland plots compared to control and upland plots while forb productivity did not differ (Table A4.1). Total ANPP and graminoid productivity responded very similarly – as expected because total ANPP is primarily made up of graminoid growth at KPBS – so I focused on total ANPP for all remaining analyses.

Irrigation transects (IrrT) – Over the entirety of the experiment (1991-2011), ANPP was significantly higher in irrigated plots (747.1 +/- 18.1 g m^{-2}; least-squares mean +/- model S.E.) than in ambient plots (532.5 +/- 16.8 g m^{-2}; TableA4.1). Plant community composition was not significantly different between treatments during the first nine years of the experiment (1991-1999) based on a permutational MANOVA (all $P > 0.1$; Table A4-2). However, starting in 2000, plant community centroids differed in every year ($P < 0.05$ except in 2004 where $P = 0.052$; Table A4-2; Fig. 3.1A). I subsequently assessed community composition for those years after the community shift had occurred to identify which species were driving differences between irrigated

and control communities. The five species contributing most to divergence of plant communities cumulatively explained 63.0% of the difference between community centroids (Table A4-3). The most important of these was *Panicum virgatum*, for which relative cover was almost 2-fold higher in irrigated (35.2 +/- 2.2%) than in ambient plots (19.6 +/- 2.2%; $F = 25.39$; $P < 0.01$). There were no significant differences in mean cover for the other four most important species: *Schizachyrium scoparium*, *Andropogon gerardii*, *Helianthus rigidus*, or *Dalea candida* (Fig. 3.1B; Table A4-4). Species richness (S) and Shannon's diversity (H') were not significantly different between irrigated and ambient plots from 1991-1999 ($F=1.78$ and 0.12, respectively; $P=0.20$ and 0.74, respectively), yet during 2000-2011 richness was marginally lesser ($F=3.56$; $P=0.07$) while H' was significantly less ($F=5.17$, $P=0.03$) in irrigated (S: 14.9 +/- 1.42; H': 1.51 +/- 0.07) versus ambient (S: 16.7 +/- 1.47; H': 1.66 +/- 0.06) plots (Fig. 3.3). Despite changes in species relative abundances and diversity, no differences in functional group abundance was found after the community shift (Table A4-5) indicating a switching of dominant C_4 grass species instead of shifts in functional group abundance. I then analyzed productivity responses separately before (1991-1999) and after (2000-2011) the community shift. The average ANPP in irrigated plots during 1991-1999 was 620.4 +/- 22.5 g m^{-2}, while the average ANPP in irrigated plots during 2000-2011 was 861.2 +/- 22.5 g m^{-2}. Average ambient 1991-2011, irrigated 1991-1999, and irrigated 2000-2011 ANPP were all significantly different from each other (Fig. 4.1c; Table A4-6).

Sensitivity of ANPP to inter-annual variation of precipitation ($ANPP_{sensitivity}$) differed for irrigated plots before versus after the community shift. It is important to note that because water was added in addition to ambient precipitation, plots were exposed to substantial inter-annual variability in total water inputs even in the irrigation transect. The slope coefficient in control plots from 1991-2011 was significantly positive (0.36 +/- 0.07; $F = 32.34$; $P < 0.01$; $R^2 = 0.14$) whereas

inter-annual variability in ANPP in the irrigated plots before the community change occurred was not related to growing season precipitation ($F = 2.16$, $P = 0.15$). However, during 2000-2011 a significant slope was detected in irrigated plots (0.59 +/- 0.29; $F = 6.64$, $P = 0.01$; $R^2 = 0.037$), and I found no significant difference between slopes of control and irrigated post-composition change plots ($F = 2.17$, $P = 0.14$; Fig. 3.2). See Table A4-6 for full model output.

Upland-lowland comparison (ULC) – Over this 29 year data set (1983-2011), ANPP in the lowlands (568.8 +/- 7.9 g m^{-2}) was significantly higher than in the uplands (378.5 +/- 7.9 g m^{-2}; $F = 17.83$, $P < 0.01$) as expected. Also as expected, plant community composition was significantly different between upland and lowland areas in every year based on permutational MANOVA (all $P < 0.01$; Table A4-2; Fig. 3.2A). The top five species contributing to divergence of upland and lowland communities cumulatively explained 63.8% of the difference between communities (Table A4-3). When I looked at these five species individually, *Panicum virgatum* cover was significantly lower in upland (4.4 +/- 1.9%) than in lowland plots (22.0 +/- 1.9%; $F = 25.39$; $P < 0.01$), *Schizachyrium scoparium* cover was significantly higher in upland (24.3 +/- 1.3%) than in lowland plots (18.5 +/- 1.3%; $F = 10.89$; $P < 0.01$), while *Andropogon gerardii*, *Sorghastrum nutans*, and *Ambrosia psilostachya* relative cover was not significantly different between lowland and upland plots (Fig. 3.2B; Table A4-4). Richness (S) and Shannon's diversity (H') were both greater ($F=43.86$ and 28.5, respectively; both $P<0.01$) in upland (S: 20.97 +/- 0.71; H': 1.87 +/- 0.04) than in lowland (S: 18.5 +/- 0.49; H': 1.74 +/- 0.03) plots (Fig. 3.3). Again, despite changes in relative abundances of species and diversity, only slight differences in functional group abundance were found after the community shift (Table A4-5). Although (1) overall ANPP was greater in lowland than in upland areas, (2) plant communities differed substantially, and (3) the ANPP-PPT relationships were both significantly positive (lowland slope coefficient: 0.30 +/- 0.08,

upland: 0.30 +/- 0.07; F = 13.0 and 20.18, respectively; both $P < 0.01$; $R^2 = 0.11$ and 0.16, respectively), I found no significant difference between $PPT_{sensitivity}$ in upland vs. lowland plots ($F = 0.06$, $P = 0.81$; Fig. 3.2C; Table A4-6).

3.4 DISCUSSION

Spatial and temporal models relating ANPP to precipitation differ fundamentally in the role played by plant communities. In temporal models, plant communities remain relatively constant over time and the relationship between ANPP and precipitation is driven by inter-annual variability in precipitation (Lauenroth and Sala, 1992). In contrast, the relationship between ANPP and precipitation in spatial (or regional) models is driven by MAP and community composition co-varying across space – with both determining ANPP. These two models are linked by the expectation that if there are long-term directional changes in precipitation (or water availability in general) at a site, community change will eventually occur (Smith et al., 2009), and thus while the temporal model may be a better predictor of ANPP responses prior to community change, the spatial model (incorporating community change) should be a better predictor of future $ANPP_{sensitivity}$. Indeed, theory predicts that with chronic changes in water availability for any particular ecosystem, responses in function (e.g., ANPP) will initially be modest, constrained by physiological responses of the extant plant community. However, as communities adjust to new resource levels, greater responses in ecosystem function will occur as species better able to take advantage of increased resource availability become more abundant (Smith et al., 2009). Recently, Collins et al. (2012) and Knapp et al. (2012) provided empirical evidence in support of this temporal link between community change and ecosystem function in response to chronic resource increases. I used two long-term data sets to test an additional prediction from spatial models – namely, that with expected change in community composition and ANPP driven by chronic

wetting or drying of an ecosystem, ecosystem sensitivity to inter-annual variability in precipitation ($ANPP_{sensitivity}$) will vary inversely with ANPP (Huxman et al., 2004; Sala et al., 2012). However, my analyses for this grassland did not support that prediction. Despite shifts in community composition to greater abundances of more mesic and productive grass species and ANPP much greater than predicted by the original temporal model in the long-term irrigation experiment, $ANPP_{sensitivity}$ did not decrease as predicted by the spatial model (Fig. 3.2C). Similarly, when comparing functionally drier uplands vs. lowlands, no change in $ANPP_{sensitivity}$ was detected. This was despite significant and relatively stable differences in community composition (Fig. 3.2A) that included increases in the abundance of species more characteristic of drier grasslands in uplands compared to lowlands (*S. scoparius*; Fig. 3.2B). Moreover, ANPP averaged ca. 200 g m^{-2} lesser in upland than in lowland sites, which is more similar to grasslands with much lesser MAP (Sala et al., 1988).

Why doesn't ecosystem sensitivity to precipitation change as predicted by regional models? I propose two hypotheses, not mutually exclusive, to explain this lack of response in $ANPP_{sensitivity}$ within this grassland. First, community traits determine and stabilize sensitivity until functional turnover occurs – the spatial $ANPP_{sensitivity}$ model is driven by dramatic differences in dominant growth forms in systems ranging from deserts to grasslands to forests, and although under chronically different water availabilities, significant shifts in community composition occurred, I found no evidence of major shifts in functional composition (i.e., C_4 grass or woody species abundances). This perhaps explains why sensitivity shifts did not align with current theory. Yet, multiple aspects of community structure can drive changes in production. Theory and empirical evidence suggest biodiversity can affect production through complementarity or redundancy of species and/or plant traits allowing the community to more fully utilize resources in dynamic

environments (Yachi and Loreau, 1999; Isbell et al., 2011). If these mechanisms were responsible for the maintenance of sensitivity despite chronically wetter conditions (where, based on the spatial model, co-limitation should be reducing sensitivity), higher levels of biodiversity should exist in the more mesic areas of our study. However, I did not find this to be the case as both richness and Shannon's diversity were lesser in irrigated and lowland plots (Fig. 3.3). Alternatively, I suggest that the lack of change in sensitivity was driven by the switch of dominant species within the same functional group and the associated switch of dominant growth-related plant traits, not biodiversity effects *per se*.

A second hypothesis that may explain the lack of shift in ANPP sensitivity is that light limitations to NPP may increase from low to high MAP, thus reducing sensitivity to water availability (Huxman et al., 2004). Within this grassland ecosystem, it appears the strengths of these drivers have not changed enough to alter sensitivity. Again, this prediction is based upon relationships across biomes with very different vegetation structures, having distinctly different plant functional types and exerting drastically different levels of water and light limitation. Deserts and semi-arid grasslands are typically characterized by low lying vegetation interspersed with frequent patches of bare ground where evaporation rates are high (Noy-Meir, 1973). Most grasslands have continuous vegetative canopy cover, which reduces the amount of evaporation occurring and increases the importance of light, while forests, having vertical structure, typically exhibit even lesser evaporation rates and even greater levels of light limitation. This is not to say the strength of drivers such as light will not respond dynamically under chronic changes in water availability, but based on the lack of sensitivity shifts I observed, I suggest that these differences are small compared to inter-biome differences.

Conclusions – My results provide insight into potential responses of ecosystem function under chronic increases in rainfall; overall productivity and initial sensitivity responses coincide with current theory suggesting that production will exceed predicted values after plant communities become better suited to new environmental conditions. To my knowledge, no studies before this have looked at temporal patterns of sensitivity due to the necessity of experiments documenting clear species reordering and that run long enough both before and after community change to assess sensitivity robustly. Based on these results, I conclude that (1) spatial models of sensitivity are likely not predictive for climate change scenarios, at least on decadal time scales, and (2) plant community change may actually stabilize this important functional relationship within biomes suggesting that in the near term, there may be less change in $ANPP_{sensitivity}$ relationships than expected despite rapid changes in water availability.

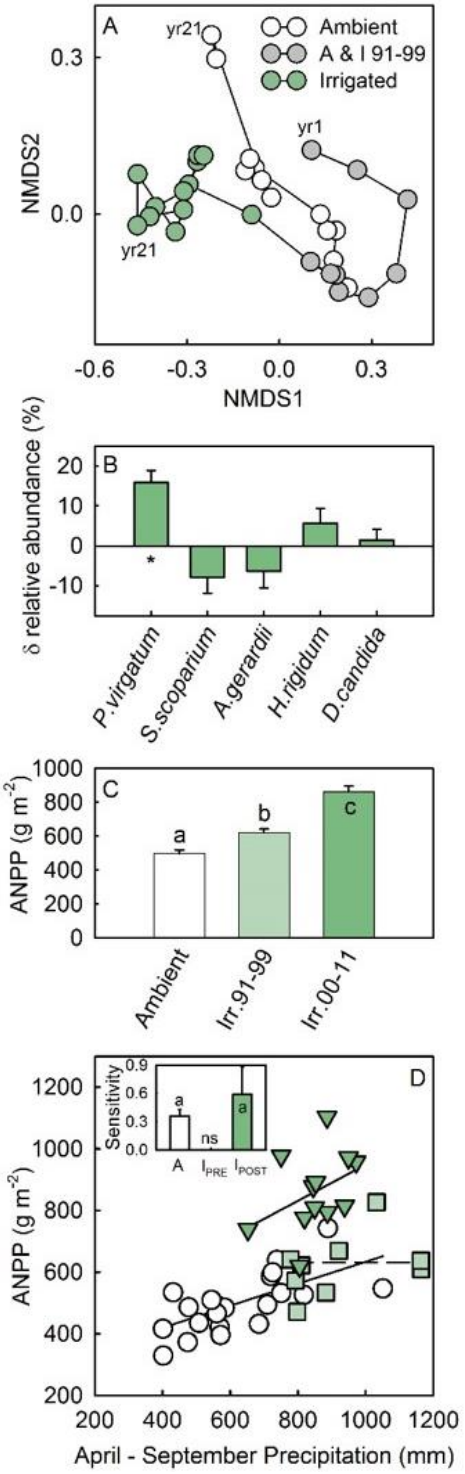

Figure 3.1. Community and productivity responses over 23 years of irrigation: **(A)** Non-metric multidimensional scaling centroids over time representing plant communities in ambient and irrigated plots together before community change (grey circles), and both ambient (open circles) and irrigated (green circles) communities after community change. Starting in 2000, communities were significantly different in every year ($\alpha = 0.05$) besides 2004 ($P = 0.052$); **(B)** Differences in relative cover between control and irrigated plots of the five species most responsible for community dissimilarity between the treatments based on similarity percentages analysis. Cover differences incorporate averaged data from all years after the communities diverged (2000-2011). Asterisks represent significant differences between average control and irrigated relative species abundance ($\alpha = 0.05$); **(C)** Average aboveground net primary productivity (ANPP) in ambient plots over the entire experiment (open bar), in irrigated plots before the plant community shift (1991-1999; light green bar), and in irrigated plots after the community shift (2000-2011; dark green bar). Different letters indicate significant ($\alpha = 0.05$) differences of least-squared means. Using two years of new data, this figure is an extension of the analysis reported in Knapp et al., (2012); **(D)** Relationship between growing season precipitation and ANPP in plots receiving ambient precipitation from 1991-2011 (open circles), ambient + irrigation during 1991-1999 (before community change; squares) and 2000-2011 (after community change; triangles). **Inset**: Ambient (A) and irrigated sensitivities calculated as the amount of productivity per unit of growing season precipitation before (I_{Pre}; 1991-1999) and after (I_{Post}; 2000-2011) community change. Different letters indicate significant differences between treatments, and error bars represent standard errors of the slope estimates.

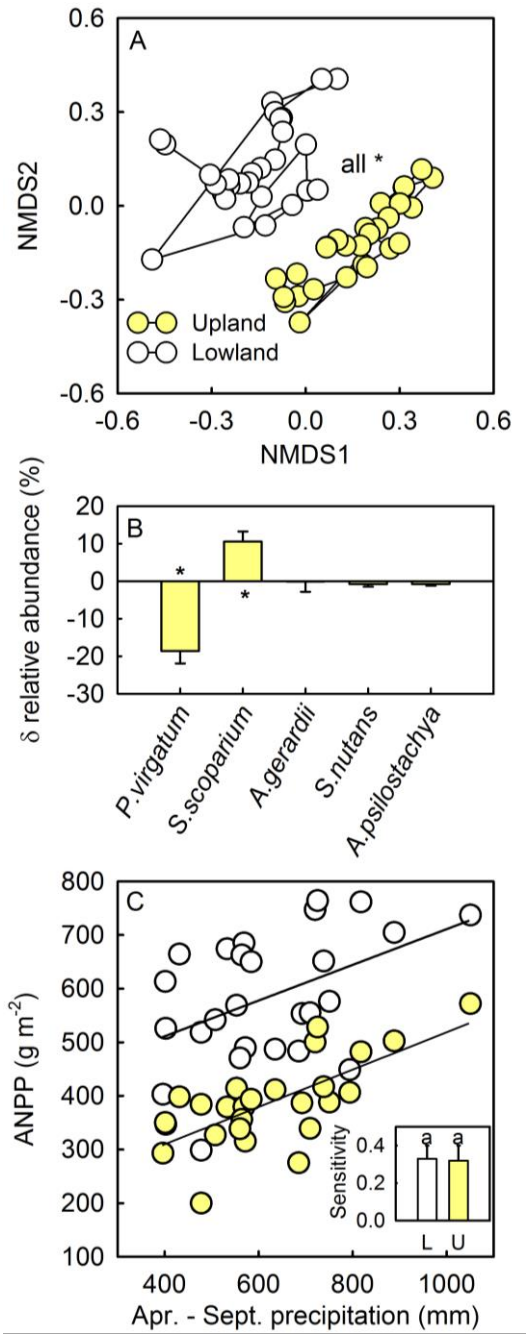

Figure 3.2. (A) Non-metric multidimensional scaling centroids over time representing upland (open circles) and lowland (filled circles) plant community composition in each year from 1983-2011. Asterisks represent significant differences ($\alpha = 0.05$) between community centroids in a given year based on a permutational MANOVA. **(B)** Differences in relative cover between upland and lowland plots of the five species most responsible for community dissimilarity between the treatments based on similarity percentages analysis. Cover differences shown are averages of data spanning 1983-2011. **(C)** Relationship between growing-season precipitation and ANPP in upland (open circles) and lowland (filled circles) plots. Although annual ANPP means are shown for clarity, analyses utilized transect level ANPP data. **Inset**: Upland (U) and lowland (L) sensitivities calculated as the amount of productivity per unit change of growing season precipitation. Different letters indicate significant differences between treatments.

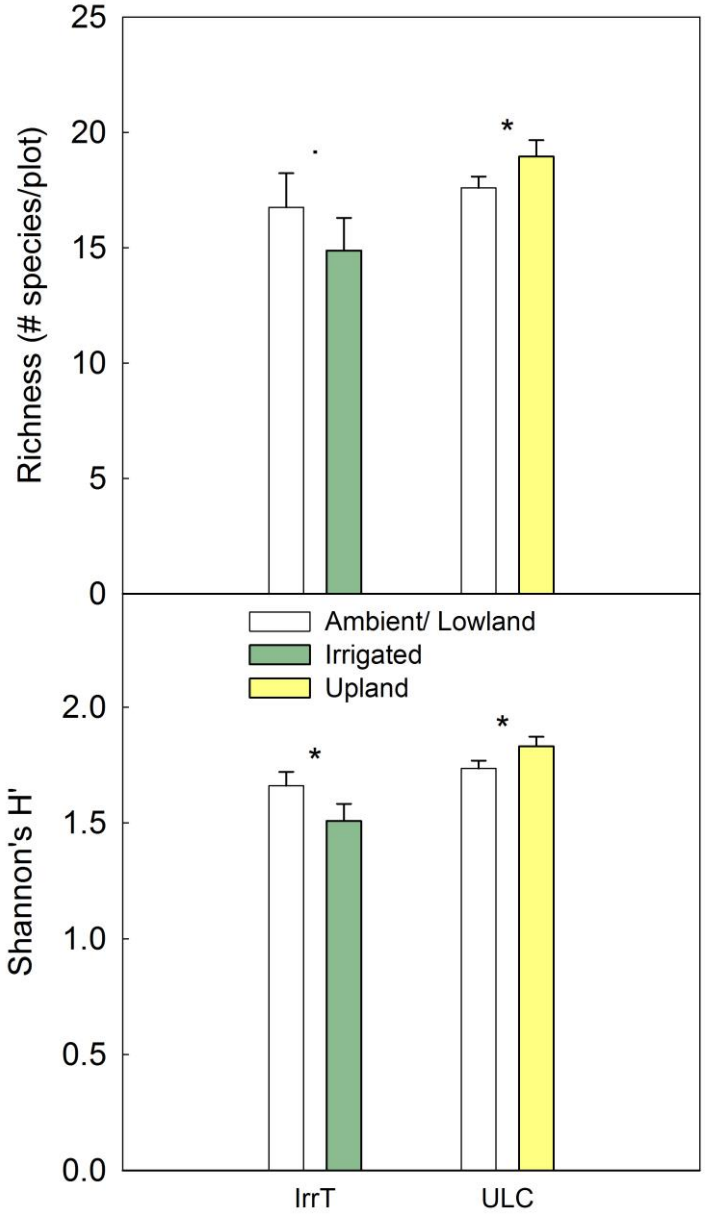

Figure 3.3. Comparison of plant species richness and Shannon's diversity in uplands and lowlands (1983-2011), and irrigated and ambient plots (2000-2011) at the Konza Prairie Biological Station, Manhattan, KS. Asterisks represent significant differences calculated using a repeated measures ANOVA at $\alpha = 0.05$ and the periods at $\alpha = 0.1$. Error bars represent standard error calculated each year and averaged across years.

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CHAPTER 4: UNEXPECTED CHANGES IN SOIL C IN A NATIVE GRASSLAND SUBJECTED TO EXTREME DISTURBANCE AND PRECIPITATION REGIMES

4.1 INTRODUCTION

There are many aspects of global change that are expected to impact ecosystem structure and function in the future, with increases in the magnitude, duration, and frequency of extremes in disturbance regimes and climate likely to have the greatest impacts (Gutschick and BassiriRad, 2013; Knapp et al., 2008; Smith et al., 2008, 2011; Reichstein et al., 2013). One global change driver likely to have substantial effects on a variety of ecosystems is an increase in fire frequency corresponding with more frequent, intense droughts and heat waves (Easterling et al., 2000). Frequent fire can also be perpetuated by plant community shifts to those well adapted to fire (Mutch, 1970), and through immigration by exotic species after disturbance (Vitousek, 1996). Additionally, fire is used as a management tool in many grasslands around the world (Knapp et al., 1998; Freckleton, 2004), and its use may increase in grasslands and savanna in the face of rapid encroachment by woody plants (Briggs et al., 2002; Bond et al., 2005; Ratajczak et al., 2012). Precipitation regimes are also expected to shift in the future causing both chronic alterations in the overall magnitude of precipitation (wetter or drier depending on geographic location: Greve et al., 2014) as well as an increase in extreme wet and dry periods (Knapp et al., 2015, Cook et al., 2015). These shifts in precipitation amounts will affect primary productivity in the majority of terrestrial ecosystems – evidenced by a number of spatial and temporal models (Sala et al. 1988, 2012; Huxman et al. 2004; Del Grosso et al. 2008) – having the potential to drastically impact various ecosystem services such as the conversion of atmospheric CO_2 into vegetative biomass and subsequent deposition of carbon into the soil (Scurlock and Hall, 1998).

During fire events, the majority of carbon (C) and nitrogen (N) contained in aboveground plant tissue is lost to the atmosphere through volatilization (Seastedt, 1988) instead of being incorporated into the soil after senescence, and this can have large consequences for both carbon sequestration and future plant growth via N loss. Indeed, a number of ecosystem models predict reductions of soil C and total N pools over time under frequent fire regimes (Ojima et al., 1990, 1994; Schimel et al., 2001). However, fire also tends to increase the proportion of primary production occurring belowground (Johnson and Matchett, 2001), having the potential to offset these N and C losses as roots die and are incorporated into the soil (i.e., root turnover). And due to the high proportional contribution of root turnover to the C pool compared with aboveground plant litter (Sulzman et al., 2005; Leppalammi-Kujansuu et al., 2014), the offsetting effect of increased belowground allocation may be great. Additionally, recent findings have shown that pyrogenic organic matter deposited after fire events is not easily utilized and respired by soil fauna and microbes, thus further stabilizing soil C pools (Preston & Schmidt, 2006; Knicker et al., 2012; Soong et al., 2014).

Chronic changes to precipitation amounts have the potential to modify how fire affects biogeochemical cycling through alterations in plant growth strategies and soil nutrient processes, especially in grasslands where growth is primary limited by water and nitrogen (Huenneke et al., 1990; Seastedt et al., 1991; Blair, 1997; Knapp et al., 2001). Under higher soil resource levels, plastic root:shoot (BNPP:ANPP) allocations have been shown to favor ANPP to increase light capture, and vice versa under more limited soil resource levels to maximize water and/or nutrient capture (Keyes & Grier, 1981; Bloom et al., 1985; Giardina et al., 2003; Gao et al., 2011). Plant community shifts may cause similar responses in root to shoot ratios under chronic changes in resource availability as different species, having differing carbon allocation strategies, become

more or less suited to new soil resource conditions (Weaver et al., 1958; D'Antonio & Mahall, 1991; Nippert & Knapp, 2007). Also, N cycling rates tend to increase with increasing soil moisture (barring anaerobic conditions), thus increasing the amount of N available for plant uptake (Matson & Vitousek, 1981; Chapin et al., 2011; Wang et al., 2006). So, under chronically increased precipitation amounts, a climate prediction for many central US grasslands (IPCC, 2013), both allocation and increased incorporation of N into plant tissue may increase the rate of C and N lost during fire events by increasing both the quality and proportional quantity of ANPP. However, this prediction remains largely untested, especially in an experimental framework.

Although many empirical studies have focused on impacts of altered precipitation regimes on ANPP (Knapp et al., 2002; Muldavin et al., 2008; Fay et al., 2011; Thomey et al., 2011; Cherwin & Knapp, 2012; Zhang et al., 2013), limited information is available for similar BNPP responses despite its importance for carbon cycling (Scurlock & Hall, 1998; Friedlingstein et al., 1999; Wullschleger et al., 2001) and other belowground processes (e.g., microbial-mediated dynamics: Wardle et al., 2004). Of the limited number of studies that *have* looked at BNPP responses to altered rainfall regimes, many have shown that BNPP sensitivity frequently does not mirror that of ANPP (Frank, 2007; Byrne et al., 2013; Wilcox et al., 2015), and often differential ANPP and BNPP responses don't align with optimal allocation theory. For example, Frank (2007) found large reductions in BNPP under drought in a northern mixed grass prairie while finding no reduction in ANPP, corresponding with a decrease in root:shoot under drier soil moisture conditions. Also, Wilcox et al. (2015; Chapter 2 of this dissertation) found that increased precipitation in a shortgrass prairie caused BNPP to increase much more than ANPP, indicating an increase in root allocation under conditions of higher water availability. These contrasts between predictions and empirical findings highlight the need for additional information about how belowground production will

respond in a chronically changing climate and how these responses will affect biogeochemical processes, especially when considered along with concurrent global changes such as increasing fire frequency.

To examine how fire and chronic changes in precipitation interact to affect belowground primary productivity, root:shoot allocation, and soil biogeochemical properties, I conducted an intensive sampling regime within an annually burned, 23-year irrigation experiment in US tallgrass prairie in 2013, also utilizing long-term productivity, community composition, and soil biogeochemical data from the experiment. This experiment represents an "extreme manipulation" designed to push the system beyond current and historical environmental conditions and potential thresholds in order to provide insight into mechanistic functions and broaden our predictive capabilities (Kayler et al., 2015). More specifically, an annual fire regime represents the highest frequency of this disturbance possible in this grassland and two decades of increased growing season precipitation inputs not only represent an historically unprecedented consecutive string of high precipitation years (average 32% increase over the entire 23 years; Knapp et al., 1998), but also represents frequent occurrence of extreme wet years (1 in 3 are statistically extreme in total amount; Collins et al., 2012 *sensu* Knapp et al., 2015). In this study, I address the following questions: How are soil biogeochemical properties affected by long-term chronic irrigation and annual fire? And, what are the biotic and abiotic mechanisms behind these biogeochemical impacts? First, I predicted that annual fire would reduce levels of C and N in the soil over time due to volatilization of these elements during fire. Second, I predicted that chronic irrigation would further reduce C and N due to a combination of increased amounts of nitrogen taken up by vegetation and greater aboveground allocation of biomass.

4.2 METHODS

Data used in this study comes from a long-term irrigation experiment at the Konza Prairie Biological Station (KPBS). KPBS is a native tallgrass prairie preserve located in the flint hills region of eastern Kansas, USA (39º09'N, 96º55W). Average annual temperature at the site is 12.5ºC (USCRN data; Diamond et al., 2013) and annual precipitation averages 835 mm. Although the majority of annual rainfall typically comes between April-September (Hayden, 1998), precipitation generally decreases in later months of the growing season when temperatures are high, resulting in substantial water stress for resident plants (Buis et al., 2009). Average aboveground net primary productivity (ANPP) at KPBS is 536 g m^{-2}, the majority of which is made up of C_4 perennial grasses, namely *Andropogon gerardii*, *Sorghastrum nutans*, *Schizachyrium scoparium*, and *Panicum virgatum*. However, much of the plant diversity is made up of less abundant annual and perennial forb species (Towne, 2002).

Irrigation transects (IrrT) – From 1991-2013, irrigation occurred in an area annually burned since 1991 and periodically burned previous to that. The area was ungrazed for over 35 years. Two 140 m transects were irrigated May-September while two adjacent ambient transects received ambient precipitation. Irrigation events occurred ca. weekly via 1 m tall high-impact rotating sprinkler heads spaced 10 m apart. Irrigation via sprinklers of this type causes a gradient of irrigation levels dependent on the distance from the irrigation line. Maximum water inputs occurred 2 m distant from the transect, 50% of maximum occurred at 9.5 m, and no water inputs occurred beyond 15 m from the irrigation line (Knapp et al., 1994; Koelliker, unpublished data). The amount of water added each week was designed to eliminate all water stress throughout the growing season as determined by potential evapotranspiration estimates using Penman combination equations conducted every 10 days. The amount of water added to plots over the

course of the growing season averaged 268.6 mm (max 1991: 469.0 mm, min 2008: 55.2 mm) corresponding with an average 32% increase in annual precipitation (max 1991: 77.4%, min 2008: 4.8%). The experiment spans a slight (ca. 7 m) topographic gradient, but I utilized long-term data solely from the upland portion for this study. For further experimental details, see Knapp et al. (1994, 2001).

In 2013, I established 30, 1 m^2 sampling plots in the upland portion of the experiment; 10 plots were placed in ambient transects (five in each transect) and 20 plots in irrigation transects, with 10 located 2 m from the watering line thus receiving full water additions (W_{100}), and 10 located 9.5 m from the watering line thus receiving ca. 50% of the added water (W_{50}). In this year, ambient plots received 783.4 mm ambient rainfall while W_{100} plots received 1100.3 mm (ambient + irrigation) and W_{50} plots received 1006.7 mm. The high level of irrigation falling on the W_{50} plots is likely due to wind patterns during certain days of irrigation. For this reason, I examined whether response variables differed significantly between W_{50} and W_{100} treatments, and when they did not, pooled these treatments for analysis (see *Statistical Analyses* section below). Ambient precipitation was measured at a weather station 200 m away from the transects, and irrigation amounts for W_{100} and W_{50} were measured using 2 rain gauges each, established at 2 and 9.5 m from irrigation lines, respectively. Gauges were maintained just above plant canopy height throughout the growing season. Growing season soil moisture – integrated from 0-15 cm – was measured hourly in 2 randomly assigned plots within each treatment using time domain reflectometry (TDR-model CS616; Campbell Scientific) probes. Probes were calibrated using three gravimetric soil samples at different time points spanning a wide range of soil moisture conditions, then converted back to volumetric soil water content using a bulk density value of 1.0 g cm^{-3} (Klute, 1986; Williams & Rice, 2007).

Long-term sampling – In September-October from 1991-2012, ANPP measurements were estimated by clipping all aboveground plant biomass in six randomly placed 0.1 m^2 quadrats at each sampling location. Subplots were averaged to obtain sampling location ANPP estimates. There were four ANPP sampling locations in the upland area of the experiment in 1991 and 1992, and 11 from 1993-2012. Biomass samples were sorted into graminoid, forb, and woody categories and dried at 60ºC for 48 hours prior to weighing. Plant species abundances were visually estimated each growing season during late July using modified Daubenmeyer cover classes (Daubenmire, 1959, Abrams & Hulbert, 1987). Four permanent 10 m^2 plots in each of irrigated and ambient treatments were sampled in 1991 and 1992, and 11 from 1993-2012. Cover classes were converted to the midpoint abundance value. Total soil C in fully irrigated and ambient areas was determined during the late growing season using 19.1 mm diameter soil cores from 0-25 cm in 1992, 1997, and 2010. Four soil cores were aggregated and homogenized for each sampling point of which there were four each in irrigated and ambient in 1992, 11 each in 1997, and five ambient and two irrigated in 2010. Total soil N was sampled from 0-5 cm in 1992, 2002, and 2010 with the same replication as the corresponding years of nitrate and ammonium sampling outlined below. Ammonium and nitrate were measured in 19.1 mm, 5 cm deep soil cores taken in the mid-to-late growing season in both irrigated and ambient areas in 1992, 1997, and 2010. 10 cores were aggregated and homogenized for each sampling location, and there were four sampling locations for both irrigated and ambient areas in 1992, 11 each in 1997, and nine irrigated and five ambient sampling locations in 2010. Aggregate samples were processed through a 4 mm sieve and additional root material removed using forceps. Total soil C in 1992 and 2010 and total soil N in 1992, 2002, and 2010 were measured via dry combustion and gas chromatography using a Carlo-Erba NA 1500 C/N analyzer (CE Instruments Ltd., Wigan, United Kingdom) and total soil C was

quantified in 1997 via conversions of Walkley-Black measurements of percent soil organic matter (%OM) content using the equation: $\%C = \frac{\%OM}{1.72}$. Nitrate and ammonium were quantified using 1M KCl extractions. All soil measurements were conducted at the Kansas State University Soils Testing Lab (Manhattan, KS, USA). For additional information on soil analyses used, see the North Central Regional Research Publication No. 221 (Revised).

2013 Sampling – In September, ANPP was estimated by clipping all aboveground vegetative biomass in two 0.1 m^2 subplots per sampling plot, which were averaged to get plot means. Samples were processed identically to those from 1991-2012. Belowground net primary productivity (BNPP) was estimated using two root ingrowth cores (Persson, 1980) per plot. Cores were 5 cm in diameter and installed 30 cm deep mid-May through September to capture the majority of root growth (Jackson et al., 1996; Nippert et al., 2012). Ingrowth cores were constructed from 2 mm fiberglass screen and filled with 2 mm sieved native soil, packed to approximate soil densities of undisturbed ground. Cores were extracted in September and kept at 4ºC until processed. Protruding roots were clipped from the outside of the mesh cores and cores were split into 0-15 cm ($BNPP_{0\text{-}15}$) and 15-30 cm ($BNPP_{15\text{-}30}$) categories. Contents within were elutriated and washed to separate soil from root biomass. BNPP samples were then sorted into soil organic matter (SOM) and BNPP categories, dried at 60º C for 48 hours and weighed. Finally, one BNPP sample from each plot (the other was saved for tissue nutrient analysis) was burned in a muffle furnace heated to 450º C for 4 hours to obtain ash mass which was subsequently subtracted from root sample measurements to calculate ash-free dry mass (AFDM). A calibration regression was created using burned samples (AFDM=0.71 x RootDryMass + 0.0156; $R^2 = 0.70$) and applied to unburned samples to estimate AFDM. Plot-level BNPP estimates were calculated averaging across both subplot estimates. Because of the destructive nature of BNPP sampling, ANPP and

BNPP samples were collected from different areas in the plot, and due to high spatial heterogeneity of root growth, overall treatment means of BNPP were divided by those of ANPP to estimate root:shoot. Standing crop root biomass (SC_{0-15} and SC_{15-30}) was sampled down to 30 cm in mid-September using a 5 cm diameter soil core, and processed identically to BNPP samples except samples were sorted into live root, dead root, and SOM categories, and all samples were burned in the muffle furnace for AFDM calculations except those used for isotopic analysis (see below). Root turnover was calculated at the plot level by dividing BNPP by maximum standing crop root biomass (Dahlman & Kucera, 1965; Gill and Jackson 2000). Although standing crop is typically at its highest in June in tallgrass prairie, the reduction in standing crop root biomass between June and October is very slight (Dahlman & Kucera, 1965), providing confidence that samples taken in September were a good proxy for maximum standing crop root biomass.

C:N was measured for root and leaf tissue from each plot via dry combustion-infrared detection of carbon (C) and thermal conductivity detection for nitrogen (N) using a LECO Tru-SPEC elemental analyzer (Leco Corp., St. Joseph, MI, USA). For leaf-level C:N, 1-2 of the newest, fully emerged leaves were clipped in each plot at the peak of the growing season (early August) from each of 3-4 individuals of *Andropogon gerardii*, a C_4 perennial grass by far the dominant species in the upland portion of the experiment. Samples were dried at 60ºC for 48 hours and ground to < 1 mm before elemental analysis. One $BNPP_{0-15}$ sample from each plot was also processed in the same way to measure root C:N. $\delta^{15}N$ and $\delta^{13}C$ were measured on the live root components of 4 randomly chosen SC_{0-15} samples in Ambient and W_{100} treatments using combustion with a CE1110 elemental analyzer (Carlo Erba Instruments, Milan, Italy) and Delta Plus mass spectrometer (Thermo Eloctron Corp., Bremen, Germany). Isotopes were measured using a ConFlo II Universal Interface (Thermo Electron Corp., Bremen, Germany). Δ values were

obtained by comparing samples to a working standard which always had a within-run standard deviation of <0.1‰. Soil available N was measured using two resin bags per plot installed early May-September. Bags were made of fine (<1 mm), undyed nylon mesh and contained 5 g each of anion exchange resin (Cl^- form; Dowex 1X8-100, 50-100 mesh) and cation exchange resin (H^+ form; 50WX8-40, Dowex HCR-W2, 8% cross linking, 16-40 mesh). The day prior to installation, bags were soaked for one hour in 0.6 N HCl then rinsed with de-ionized water three times and stored at 4ºC. Bags were buried at opposite corners of plots 10 cm deep. Measurement of available N (nitrate and ammonium) bound to resins was accomplished by first extracting N by shaking resin bags in 100 ml of 2 M KCl at 200 rpm for 2 hours and processing the solution through polycarbonate filters. Concentration of N in extracts was then measured using an Alpkem Flow Solution 4 Automated Wet Chemistry System (O.I. Analytical, College Station, TX, USA).

Statistical analyses – 1991-2012 ANPP was compared between irrigated and ambient plots using a repeated measures mixed effects ANOVA with an autoregressive covariance matrix, chosen using corrected AIC, and transect as a random effect. Temporal trends of soil C and total N were analyzed using year as a continuous variable in a mixed effects model with transect as a random effect, and differences between irrigated and ambient values in each year were examined using Tukey-adjusted multiple comparisons of least-squared means. Long-term community composition was analyzed yearly from 1991-2012 using permutational MANOVA in R (*adonis* function in the vegan package). Similarity percentage analysis (*simper* function in the vegan package) was used to distinguish which species were most driving differences in species composition. This was done for each year individually when community composition was significantly different as well as by pooling all years after the community began to change. 2013 growing season soil moisture differences were examined using a repeated measures ANOVA with

day of year as the repeated effect and autoregressive heterogeneous covariance structure. 2013 data describing grass biomass, forb biomass, woody biomass, ANPP, BNPP, total NPP, standing crop root biomass, root turnover, root C:N, leaf C:N, and soil inorganic N were compared among ambient, W_{50}, and W_{100} treatments using a mixed effects model with transect as a random effect and treatment as a fixed effect. Depth was included as an additional fixed effect in BNPP and standing crop root biomass models. Additionally, contrasts were run within the above 2013 models comparing W_{50} and W_{100} to determine whether significant differences existed. Because no significant differences were found between W_{50} and W_{100} for any response variables (Table 4.1), contrasts were run comparing pooled W_{50}, W_{100} (W) plots with the ambient. Differences in $\delta^{15}N$ and $\delta^{13}C$ data were examined between ambient and W_{100} using a mixed effects model with transect as a random effect. Permutational MANOVA, and analysis of similarity percentages were run using the vegan package in R (v 3.1.2; R Foundation for Statistical Computing; Vienna, Austria), while all other analyses were conducted using SAS (v9.3; SAS Inst.; Cary, NC, USA).

4.3 RESULTS

Over the 22 years of the experiment prior to sampling in 2013 (i.e., 1991-2012), water falling on irrigated plots (1101 +/- 131 mm: μ +/- standard deviation) was 30.9% higher than the ambient (842 +/- 177 mm), and 2013 irrigation was similar to these long term trends (Fig. 4.1). Although 2013 season-long average soil moisture was not significantly different between irrigated and ambient plots ($F=0.20$, $P=0.82$) – likely due to a combination of high temporal variability as well as low replication in ambient plots ($n=2$) – increases in soil moisture tracked irrigation events well, maintaining elevated soil moisture conditions throughout the majority of the growing season, while ambient plots experienced extended periods of lower soil moisture conditions (Fig. 4.1).

I looked closely at temporal dynamics of total soil N and C after the initiation of an annual fire regime in 1991, as well as how chronic irrigation modified these effects. Specifically, I looked for evidence of a reduction in soil C and N as predicted by ecosystem models (Ojima et al., 1990; Schimel et al., 1991). Total N in 0-5 cm soil samples showed no significant trend over time in ambient plots as well as no significant differences between irrigated and ambient plots in any one year, although I did find a negative trend of total N over time in irrigated plots (Fig. 4.2A; Table 4.2). I found a 52% increase in soil C from 1992-2010 in ambient plots, and a 19% increase in soil C in irrigated plots over this same time period. I found slight evidence of differences between ambient and irrigated soil C slopes through time (i.e., P=0.08 for the interaction term in the mixed ANCOVA; Fig 4.2B), yet there were no significant differences of soil C between irrigated and ambient treatments in any one year (Table 4.2).

Species composition was not significantly different between ambient and irrigated treatments from 1991-1995. Starting in 1996, irrigated and ambient communities began to diverge based on permutational MANOVA, and by 2001 communities were consistently different throughout the remainder of the experiment (Table A5-1). Pooling community data after community composition began to shift (1996-2011), similarity percentage analysis identified differences in irrigated and ambient communities to be driven primarily by relative covers of *Solidago canadensis* (Amb:4.1%, Irr:16.1%), *Andropogon gerardii* (Amb:40.0%, Irr:33.1%), *Panicum virgatum* (Amb:8.2%, Irr:10.5%), *Sorghastrum nutans* (Amb:14.1%, Irr:9.1%), *Amorpha canescens* (Amb:13.4%, Irr:15.7%), and *Schizachyrium scoparium* (Amb:3.9%, Irr:3.3%; ordered by level of contribution and collectively explaining 74% of the variance in species composition between treatments; Table 4.3). When analyzed by year, these same species were consistently

important; in all years after the community shift, at least 5 of the species above were identified as in the top 6 species contributing to community differences (Table A5-2).

I found no evidence of differences of C:N in live root tissue (F=0.37, P=0.55) or in leaf tissue of the dominant plant species present, *A. gerardii* (F=1.58, P=0.29) between irrigated (root: 51.4 +/- 13.1; leaf: 55.5 +/- 10.0) and ambient (root: 48.3 +/- 13.5; leaf: 48.3 +/- 3.8) plots (Fig. 4.3). However, there were marginally significant differences in $\delta^{15}N$ between treatments: roots from irrigated plots had higher values of $\delta^{15}N$ (i.e. were more enriched in ^{15}N; -0.88 +/- 0.16‰) than ambient plots (-1.34 +/- 0.40‰; F=4.49, P=0.08; Fig. 3), indicating faster rates of nitrogen mineralization in irrigated soils (Hart et al., 1994; McCulley et al., 2009). However, I found no difference between $\delta^{13}C$ values in irrigated (-14.8 +/- 1.31‰) versus ambient (-17.2 +/- 2.16‰; F=2.21, P=0.28) live roots. In 2013, no difference was detected in cumulative season-long nitrate concentrations as measured using resin bags in irrigated (0.27 +/- 0.16 µg/10g resin bag) versus ambient (0.25 +/- 0.16 µg; F=0.27, P=0.61) plots. However, marginally greater concentrations of ammonium were bound to resin bags in irrigated (0.98 +/- 0.82 µg) versus ambient (0.69 +/- 1.1 µg; F=3.33, P=0.08) plots. In addition, soil samples from 0-5 cm were taken in 1992, 1997, and 2010 in which nitrate and ammonium concentrations were measured. Over the three time periods, ammonium concentrations were significantly higher in irrigated (4.53 +/- 5.14 µg per g of soil) versus ambient plots (1.91 +/- 1.48 µg g^{-1}; F=22.05, P=0.02; Fig 4.3D), although the effect varied by year (F=47.92, P<0.01; Table 4.2). Alternately, nitrate was not significantly different in irrigated (3.08 +/- 3.97 µg g^{-1}) and ambient plots (2.72 +/- 2.65 µg g^{-1}; F=0.01, P=0.92; Fig. 4.3D), yet again the effect varied by year (F=5.50, P=0.02).

From 1991-2012 overall, ANPP was 43.9% higher in irrigated plots (683.7 +/- 152.9 g m^{-2}) versus ambient (475.1 +/- 117.4 g m^{-2}; F=25.9, P=0.03; Fig. 4.1c), but in 2013, I found no

significant difference of ANPP in irrigated (557.2 +/- 139.3 g m^{-2}) versus the ambient (551.0 +/- 163.7 g m^{-2}; F=0.01, P=0.93; Fig. 4.1). This lack of ANPP response in 2013 is not unusual in this mesic grassland; in 11 out of 22 years between 1991 and 2012, ANPP responses were not significantly different between treatments at α=0.05 (6 out of 22 years not significant at α=0.1). Despite this lack of significant difference of ANPP in 2013, BNPP was 20.6% less in irrigated plots (414.3 +/- 111.3 g m^{-2}) relative to the ambient (521.6 +/- 154.5 g m^{-2}; F=4.63, P=0.04). Although I found significantly greater levels of BNPP in shallower soil levels (0-15 cm; 265.3 g m^{-2} +/- 71.1) compared with deeper soils (15-30 cm; 171.2 +/- 66.4 g m^{-2}; F=28.14, P< 0.01), there was no evidence for changes in the depth at which BNPP occurred in irrigated versus ambient (Depth*Treatment: F=0.42, P=0.66). The lack of change in ANPP along with a concurrent reduction in BNPP in irrigated plots corresponded with a 26% reduction of the root:shoot ratio in irrigated plots versus ambient (Fig. 4.4A inset). Surprisingly, despite reductions in BNPP, I found no differences between standing crop root biomass in irrigated (982.1 +/- 200.9 g m^{-2}) versus ambient plots (931.9 +/- 159.2 g m^{-2}; F=0.38, P=0.58), and by incorporating plot-level BNPP and standing crop root biomass, I estimated that root turnover rates were lower in irrigated plots (0.45 +/- 0.21) relative to ambient (0.57 +/- 0.16; F=3.71, P=0.06; Fig 4.4). Similar to BNPP, standing crop root biomass was greater in shallow (604.1 +/-144.6 g m^{-2}) versus deep (361.27 +/- 143.6 g m^{-2}; F=2.20, P=0.12) soils with no change in the depth distribution of standing crop root biomass between treatments (Table 4.1).

4.4 DISCUSSION

By incorporating extreme chronic increases in precipitation and a severe disturbance regime (annual fire) for over two decades, this experiment pushed the system past historical environmental thresholds at which novel ecosystem responses are likely to occur (Kayler et al.,

2015), and I was able to quantify responses of slowly changing, yet important, attributes of ecosystems such as community structure and soil C pools. Both the magnitude and temporal length of manipulations make this experiment valuable as a source of information to test current ecosystem models and inform new ones, a process sorely needed to accurately predict future biogeochemical cycles (Luo et al., 2014). In this study, I tested two hypotheses based on previous ecosystem model predictions. First, I hypothesized that initiation of an annual burning regime would result in losses of soil C and soil total N over time due to volatilization of these elements incorporated in aboveground vegetation each spring during fire events. Second, that chronic irrigation would result in further reduction of these pools as plants in wetter soils began to allocate more biomass above than belowground. As belowground plant biomass tends to contribute much more to soil C than senesced litter (Kuzyakov & Domanski, 2000; Sulzman et al., 2005; Leppalammi-Kujansuu et al., 2014), I expected that the impacts of plant allocation shifts on soil C pools would be great. I found no support for the first hypothesis: there was no change in total soil N over time in plots receiving ambient rainfall and burned annually, and in fact, a substantial increase of soil C was measured. Although these results coincide with some studies looking at the effects of fire frequency on soil C pools (Chen et al., 2005; Knicker et al., 2012), they conflict with recent findings from South African savanna grasslands showing reductions of soil C and N pools under annual fire frequencies (Pellegrini et al., 2015). One reason for this discrepancy could be that this latter study focused on areas with grazing herds; grazing has been shown to reduce belowground primary production and biomass (Ruess et al., 1998; Koerner & Collins, 2014), thus potentially offsetting mechanisms such as increased root allocation (Hartnett, 1987; Johnson & Matchett, 2001) responsible for stabilizing C in frequently burned systems. Our results agree with previous work highlighting the greater importance of root than aboveground inputs to C pools

(Sulzman et al., 2005; Leppalammi-Kujansuu et al., 2014). Fire-induced allocation responses may be due to plastic responses of vegetation (Johnson & Matchett, 2001), shifts in plant species composition resulting in increases in plant species well adapted to fire and having large belowground components (e.g., *A. gerardii*; Weaver, 1958), or due to genotypic shifts to those with different allocation strategies (Avolio et al., 2013). Background climate change variables such as increasing atmospheric CO_2 concentrations and N deposition rates may also be contributing to the lack of biogeochemical loss through increased C inputs via increased fine root turnover (Lichter et al., 2005, but this phenomenon may not be ubiquitous - see Heath et al., 2005) and N inputs through both wet and dry deposition (Goulding et al., 1998; Galloway et al., 2004). Thirdly, the formation of pyrogenic carbon during fire events could be facilitating additional C gain in the system as it has remarkably long turnover times in the soil (Knicker et al., 2012; Soong et al., 2014).

Although I found increased N mineralization and available N under elevated soil moisture conditions, I found no evidence for increased N content in either root or leaf tissue, not overly surprising as the dominant species, *A. gerardii*, has been shown to maintain stable tissue N despite large changes in soil available N (Yu et al., 2015). The combination of stable concentrations of N in plant tissue and long-term increases in ANPP (Fig. 4.1) suggests that the amount of N allocated aboveground is likely higher overall, and the associated loss through annual volatilization may be responsible for the negative temporal trend of total N with irrigation. However, despite this trend, soil N in irrigated plots was not much lower than that of plots receiving ambient precipitation, even after 20 years. Plants, especially those adapted to frequent fire, tend to translocate nutrients from their leaves to other organs more resistant to loss, such as roots and rhizomes, before senescence (Vitousek, 1982). Since fire was initiated each year in the spring (long after leaf senescence the

previous fall) during the experiment to reflect common land manager practices (Collins & Wallace, 1990), this may be a stabilizing mechanism for N pools in these ecosystems despite the occurrence of annual fire.

The slower accumulation of C and reduced BNPP inputs found in irrigated plots partially supports our second prediction, that chronic irrigation would reduce the carbon sequestration capability of the system by altering vegetative allocation strategies counter to those typically caused by annual fire. Although plastic responses may be partly responsible for the altered allocation patterns found, I also suggest that the change in species composition that occurred between 1996 and 2001 may have contributed. In this same experiment, Collins et al. (2012) found that the changes in species composition were mostly due to a switch of the dominant species *A. gerardii* to *P. virgatum*. *P. virgatum* typically has much sparser belowground root standing crops and less production typically allocated to root growth than *A. gerardii* (Weaver, 1958). Additionally, I found higher abundances of *Solidago canadensis*, a C_3 forb species that tends to have higher concentrations of roots at deeper soil levels (Nippert & Knapp, 2007), resulting in lower levels of BNPP and likely soil C levels in our samples that were only taken to 30 and 25 cm depths, respectively. As a second potential mechanism for slower C sequestration, I found evidence for reduced root turnover rates in irrigated plots, indicating reduced C inputs. Past evidence has shown that dry soil conditions can promote root turnover as plants invest in new roots to exploit new regions of soil for water and/or nutrients, and replacing roots experiencing mortality due to dry soil conditions (Sims & Singh, 1978; Santantonio & Hermann, 1985). Indeed, in 2013 there were two, ca. two week periods of time when soil moisture in irrigated plots was substantially elevated above that of ambient plots (Irr > 20% and Amb < 20% during DOY 189-206 and DOY 242-254; Fig. 4.1B). This pattern was not unique to 2013: during the growing seasons of 2007-

2012 (i.e., years for which daily soil moisture measurements were available), ambient plots experienced ca. 91% more days of < 20% soil moisture than did irrigated plots (Wilcox, unpubl. data). Thirdly, previous research has shown increased microbial activity and CO_2 respiration with irrigation in this same experiment (Knapp et al., 1998), representing yet another potential reduction in soil C through increased outputs. Despite evidence for all three of these mechanisms of soil C loss, plots receiving irrigation and annual burning still accumulated soil C over time, reflecting the high level of resistance of this system to biogeochemical loss.

As global change continues to alter ecosystem drivers like fire frequency and precipitation amounts, information concerning how these will interact to affect the functioning and services of ecosystems will be integral for formulating accurate predictions of future ecosystem states. Using a 20+ year irrigation study coinciding with the initiation of an annual burn regime, I found no support for the prediction that soil C and N would decrease under more frequent fire regimes. However, I did find evidence that chronic water additions may reduce the rate of soil C accumulation, and was associated with a negative temporal trend of total soil N. These responses were likely due in part to reduced inputs through less allocation of biomass belowground and slower root turnover rates combined with the annual volatilization of aboveground plant tissue. However, I posit that aspects of the vegetation in this ecosystem at least partially counteract the effects of irrigation on biogeochemical properties. The dominant grasses at this site allocate a large proportion of their biomass to root growth, maintain relatively high levels of biomass belowground (Weaver, 1958), and translocate a large proportion of N from aboveground to belowground tissue during senescence. Each of these properties may be an important mechanism behind the stability of this system. This work highlights the need to examine multiple global change drivers simultaneously, as their effects can interact resulting in novel ecosystem responses. Additionally,

as has been recently stated by Luo et al. (2014), I suggest that verifying and informing ecosystem models using data from long-term experiments, such as this, is vital for formulating accurate predictions of ecosystem functioning during a time of drastic global change.

Table 4.1. Model results from mixed effects ANOVAs comparing dependent variables between ambient, W50 and W100 plots in 2013 at the Konza Prairie Biological Station, Manhattan, KS, USA.

			Overall model			Partial vs full water			Ambient vs P/F pooled		
	Response variable	Effect	Df num,den	F	P	Df num,den	F	P	Df num,den	F	P
Above ground prod.	ANPP n woody	Treatment	2,3	0.13	0.88	1,3	0.26	0.64	1,3	0.00	0.98
	ANPP w woody	Treatment	2,3	0.17	0.85	1,3	0.33	0.61	1,3	0.01	0.93
	Grass	Treatment	2,3	0.08	0.92	1,3	0.08	0.79	1,3	0.08	0.79
	Forbs	Treatment	2,3	1.16	0.33	1,3	2.06	0.16	1,3	0.27	0.61
Belowground production and biomass		Treatment	2,3	2.39	0.11	1,3	0.15	0.70	1,3	4.63	0.04
	BNPP 0-30	Depth	1,51	28.15	<0.01	-	-	-	-	-	-
		Trt x Depth	2,51	0.42	0.66	-	-	-	-	-	-
	BNPP 0-15	Treatment	2,3	0.51	0.65	1,3	0.38	0.58	1,3	0.63	0.49
	BNPP 15-30	Treatment	2,3	0.82	0.45	1,3	0.09	0.77	1,3	1.54	0.22
		Treatment	2,3	0.21	0.82	1,3	0.03	0.87	1,3	0.38	0.58
	Std. crop 0-30	Depth	1,51	43.35	<0.01	-	-	-	-	-	-
		Trt x Depth	2,51	2.20	0.12	-	-	-	-	-	-
	Std. crop root 0-15	Treatment	2,3	0.57	0.62	1,3	1.12	0.37	1,3	0.02	0.89
	**Std. crop 15-30	Treatment	2,27	1.22	0.31	1,27	1.74	0.20	1,27	0.70	0.41
Leaf	Leaf C:N	Treatment	2,3.07	1.22	0.41	1,2.96	0.85	0.43	1,3.19	1.58	0.29
Root properties	Root turnover	Treatment	2,27	2.09	0.14	1,27	0.47	0.50	1,27	3.71	0.06
	**Live root N	Treatment	2,26	1.34	0.28	1,26	2.39	0.13	1,26	0.33	0.57
	Live root C	Treatment	2, 26	1.24	0.30	1,26	0.77	0.39	1,26	1.65	0.21
	**Live root C:N	Treatment	2, 26	1.79	0.19	1,26	3.13	0.09	1,26	0.37	0.55
	**δ15N *	Treatment	1, 6	4.49	0.079	-	-	-	-	-	-
	**δ13C *	Treatment	1,2	2.21	0.28	-	-	-	-	-	-
Soil Prop.	**Soil NO3	Treatment	2,27	0.59	0.56	1,27	0.91	0.35	1,27	0.27	0.61
	Soil NH4	Treatment	2,27	1.67	0.21	1,27	0.00	0.99	1,27	3.33	0.08
	Soil tot. avail. N	Treatment	2,3	0.97	0.47	1,3	0.23	0.67	1,3	1.71	0.28

* 4 random BNPP 0-15 cm chosen for isotopic analysis in ambient and full watered plots

** Log transformed for normality

Table 4.2. Model results from repeated measures mixed effects ANOVAs comparing dependent variables between ambient and fully irrigated plots during 1991-2012 at the Konza Prairie Biological Station, Manhattan, KS, USA. Also shown are Tukey-adjusted comparisons of irrigated and ambient values for each year, and Tukey adjusted P values for ambient and irrigation measurements between years for soil C and total soil N.

			Overall model			Irrigation effect each year			Trends over time		
	Response variabdle	Effect	Df num,den	F	P	Year	t value	Tuk P	Year comp.	Amb. P	Irr.P
Available N	**NO_3 0-5 cm	Treatment	1,1.79	2.67	0.26	1992	-0.58	0.99	-	-	-
		Year	2,14.8	59.53	<0.01	1997	5.21	<0.01	-	-	-
		Trt x Year	2,14.8	10.93	<0.01	2010	0.07	1.0	-	-	-
	NH_4 0-5 cm*	Treatment	1,3	21.81	0.02	1992	0.03	1.0	-	-	-
		Year	2,16.7	186.0	<0.01	1997	1.19	0.84	-	-	-
		Trt x Year	2,16.7	49.67	<0.01	2010	-12.69	<0.01	-	-	-
Total N	Total N 0-5 cm	Treatment	1, 17.1	0.00	0.97	1992	-1.55	0.63	92vs02	0.17	<0.01
		Year	2,16.7	20.56	<0.01	2002	0.00	1.0	92vs10	0.99	<0.01
		Trt x Year	2,16.7	8.31	<0.01	2010	1.87	0.44	02vs10	1.0	0.99
	Total N 0-25 cm	Treatment	1,5.99	0.22	0.65	1992	-2.42	0.13	92vs10	0.047	0.78
		Year	2,5.99	1.03	0.35	2010	1.37	0.54			
		Trt x Year	2,5.99	5.62	0.06						
Total C	Total C 0-25 cm	Treatment	1,1.92	0.05	0.84	1992	-1.83	0.46	92vs97	0.21	0.90
		Year	2,27.6	7.57	<0.01	1997	0.88	0.95	92vs10	<0.01	0.91
		Trt x Year	2,27.6	3.57	0.04	2010	0.60	0.99	97vs10	0.04	0.38

Table 4.3. Similarity percentage analysis showing the species most responsible for differences between ambient and irrigated plant communities. Analyses were run collectively for all years after the community began to shift (1996-2011). Only species cumulatively contributing 90% to divergence of communities are shown.

Genus	species	Ambient rel.cov.	Irr rel. cov.	Contribution	Cumulative contribution
Solidago	*canadensis*	0.040322	0.160567	0.169594	0.169594
Andropogon	*gerardii*	0.399458	0.330592	0.153871	0.323465
Panicum	*virgatum*	0.081731	0.105989	0.130945	0.454411
Sorghastrum	*nutans*	0.141356	0.090509	0.116777	0.571187
Amorpha	*canescens*	0.135896	0.157156	0.11338	0.684567
Schizachyrium	*scoparium*	0.039009	0.03283	0.055142	0.739709
Ambrosia	*psilostachya*	0.028687	0.01713	0.040403	0.780112
Aster	*ericoides*	0.025493	0.011719	0.032643	0.812755
Sporobolus	*asper*	0.012415	0.016619	0.022009	0.834763
Cornus	*drummondii*	0.008327	0.007918	0.016109	0.850873
Carex	*spp.*	0.012869	0.00672	0.015419	0.866292
Rosa	*arkansana*	0.002246	0.011879	0.01348	0.879772
Schrankia	*nuttallii*	0.007416	0.006201	0.01193	0.891702
Bouteloua	*curtipendula*	0.011058	0.001894	0.011306	0.903008

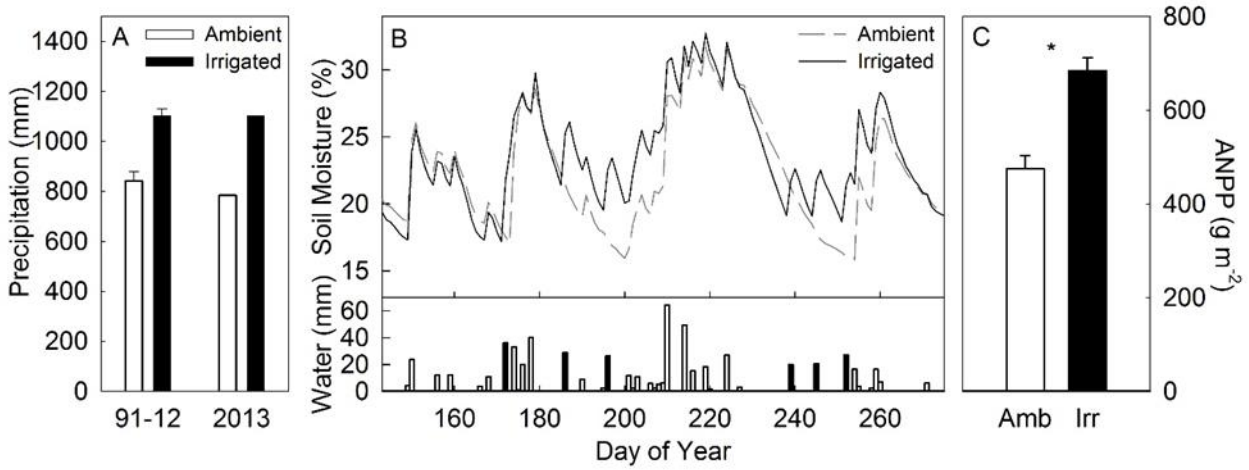

Figure 4.1. Precipitation, soil moisture, and aboveground net primary production (ANPP) in irrigated versus ambient plots from 1991-2012 compared with 2013 at the Konza Prairie Biological Station, Manhattan, KS, USA. **A**: Open bars represent average ambient annual precipitation for 1991-2012 and annual precipitation in 2013. Filled bars represent ambient annual rainfall + irrigation during the same time periods. **B**: Upper panel shows daily volumetric soil moisture 0-15 cm in ambient (dashed) and irrigated (solid) plots during the 2013 growing season. Lower panel shows ambient rainfall (open bars) and irrigation amounts (filled bars), **C**: Average ANPP in ambient (open bars) and irrigated (filled bars) plots from 1991-2012. Asterisks represent significant differences between treatments at α=0.05 and error bars represent standard error.

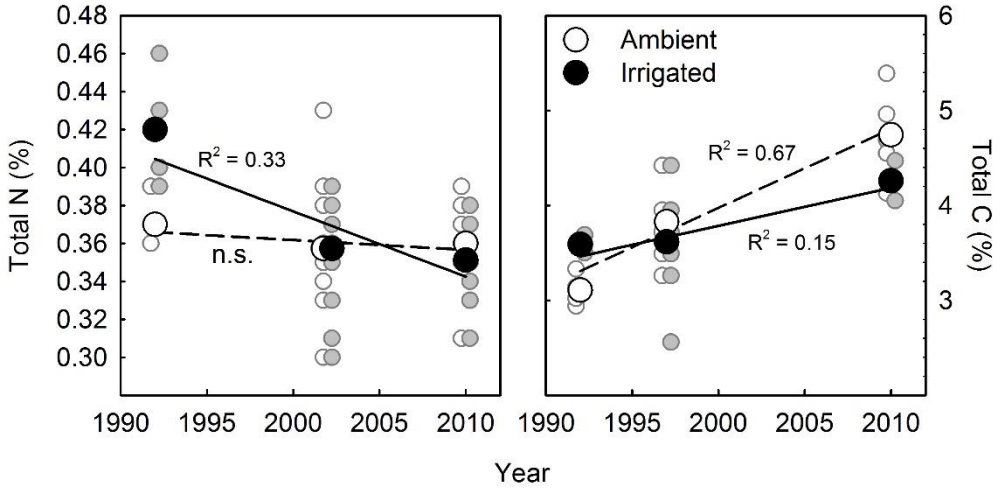

Figure 4.2. Total soil N (left) and C (right) in irrigated (filled circles, solid trendline) and ambient (open circles, dashed trendline) plots after initiation of annual fire regime in 1991 at the Konza Prairie Biological Station, Manhattan, KS. Smaller grey symbols show individual plot values of aggregate soil samples and larger symbols show annual means for each treatment. Total N was measured in ten aggregated 0-5 cm cores per plot while total C was measured in four aggregated 0-25 cm soil cores per plot.

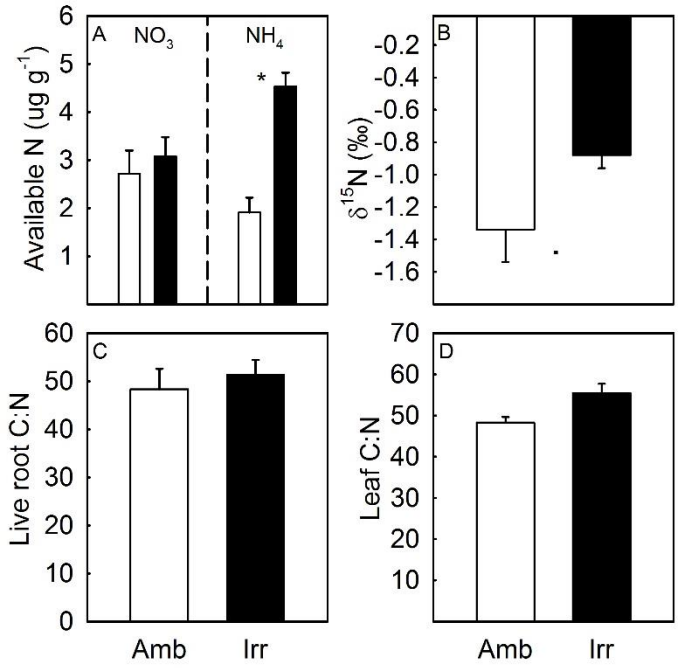

Figure 4.3. Biogeochemical characteristics of ambient (open bars) and irrigated (filled bars) plots at the Konza Prairie Biological Station, Manhattan, KS. **A**: Nitrate and ammonium concentrations were measured on 0-5 cm deep soil samples taken in 1992, 1997, 2002, and 2010 – values shown are averaged over all years. $\delta^{15}N$ (**B**) and live root C:N (**C**) were measured using live root samples taken in early September, 2013, while leaf C:N (**D**); from *A. gerardii*) was measured using samples collected during the first week of August, 2013. Asterisks represent significant differences at α=0.05 and "." Indicates differences at α=0.1. Error bars represent standard error from the mean.

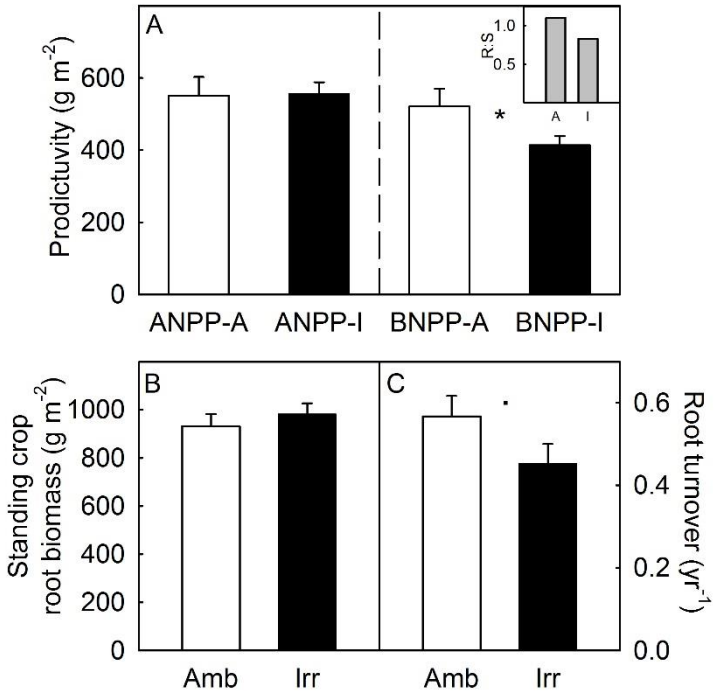

Figure 4.4. Net primary productivity (**A**), split into aboveground (ANPP) and belowground (BNPP) categories, standing crop root biomass (**B**), and root turnover rates (**C**) in ambient (open bars) and irrigated (filled bars) plots measured in 2013 at the Konza Prairie Biological Station, Manhattan, KS, USA. Panel A inset: Root:shoot was calculated by dividing the treatment means for BNPP by those of ANPP. Significant differences between irrigated and ambient plots are indicated with an asterisk for α=0.05 and with a "." for α=0.1. Error bars represent standard error from the mean.

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CHAPTER 5: CONCLUSIONS

Ecosystems provide many services important for a variety of human interests, ranging from economic to aesthetic, and global change will likely have large impacts on these benefits. Elucidating the mechanisms driving ecosystem changes is important for understanding future functioning and services provided by ecosystems. Ecosystem attributes such as edaphic properties, resource availability, and plant community composition control sensitivity across systems, and these sensitivities will likely change over time as intrinsic ecosystem properties shift under chronic alterations of climatic conditions (Smith et al., 2009). Plant community composition can impact sensitivity in a number of ways: first, biodiversity *per se* can alter productivity through complementarity effects, having a variety of species and/or functional groups occupying a large proportion of available niches and more fully utilizing available resources (Loreau et al., 2001); second, plant community composition can affect sensitivity through the identity and traits of species making up the majority of production (i.e., dominant species; Grime, 1998; Smith & Knapp, 2003); and third, through the identity of the dominant functional type which can have very different water use or acquisition strategies (deep rooted shrubs versus shallow rooted grasses; Nippert & Knapp, 2007). In addition to the effects of plant communities on ecosystem sensitivity, abiotic conditions, such as nutrient availability can control sensitivity through co-limitation (Huxman et al., 2004). Both soil nutrient levels and plant community composition are likely to themselves change under altered precipitation regimes due to various mechanisms such as altered microbial activity under different levels of soil moisture (Haynes et al., 1986), leaching of soluble nutrients (Hedin et al., 1995), and altered competition coefficients among species/functional groups as resource availabilities change (Tilman, 1982). To explore how sensitivity of ecosystems

may change in future global change scenarios, I addressed three major questions in this dissertation: (1) How does community composition, both functional and species level differences, control sensitivity of primary productivity to altered rainfall regimes? (2) Does the sensitivity of belowground net primary productivity (BNPP) mirror that aboveground (ANPP)? (3) How does sensitivity of ANPP and BNPP affect biogeochemical properties? In the remainder of this chapter, I will address these three questions using results from previous chapters, and discuss broader implications of this work in how it should inform future theoretical, empirical, and modeling efforts.

Plant communities and sensitivity – I looked at how plant community structure influences the sensitivity of primary production in chapter 2 and chapter 3. In chapter 2, I showed patterns of sensitivity to increased precipitation across 3 grassland types, which varied in functional composition (two C_4 and one C_3 dominated system) and also spanned a productivity gradient. In this experiment, I found ANPP was more responsive to water additions in the more mesic of the two C_4 dominated grasslands, and that the C_3 dominated northern mixed grass prairie showed the lowest sensitivity of all three sites, despite it having productivity levels intermediate between the two C_4 dominated grasslands. In chapter 3, I used data from a long-term irrigation experiment in tallgrass prairie, which experienced a shift in plant abundances after nine years of water additions; the community shift did not incorporate a change in plant functional types, but simply a shift of the dominant species to a more mesic assemblage of C_4 grasses. I found that sensitivity to precipitation was initially reduced under high levels of water availability, yet after the community shift occurred, sensitivity was restored.

The lack of sensitivity I found in the C_3 dominated northern mixed grass prairie (eastern Montana) in chapter 2 was likely related to the timing of growth of the C_3 graminoids in the system.

These plants typically complete the majority of their growth during the spring season when soils are saturated from snow melt. For this reason, additional water during this time period likely has little effect on primary production; even in more southerly C_4 grasslands, there is evidence that soil moisture dynamics tend to have the largest impact during later periods of the growing season, when soil moisture levels are low (Denton et al., 2014). And in a C_3 dominated system, additional water availability during these drier late season periods occur after plant growth has mostly ceased (Vermiere et al., 2008; Ehrlinger, 2005) resulting in a lack of sensitivity to increased precipitation.

When looking at the two C_4 grasslands in this study, I found sensitivity of ANPP to water additions was higher in communities comprised of more mesic species across a rainfall/productivity gradient. This finding does not fit within regional models showing reduced sensitivity in more mesic systems, attributed to co-limitation by resources other than water (Huxman et al., 2004). An alternate driver of sensitivity may be the traits of the plant community present in a system. In lower productivity ecosystems, aboveground production is often capped by growth limitations of resident plants species (Knapp & Smith, 2001); indeed, many shortgrass prairie species reach maximum heights of less than half a meter, even in wet years. When contrasted with species that dominate more mesic grasslands, which can grow to over 2 m in height, it is easy to see how the traits of species in an ecosystem may drive sensitivity in an opposite direction from that of co-limitation. However, in response to chronic changes in precipitation amounts, shifts in the dominant plant species can occur, and based on my findings from chapter 2, I predicted that changes in ecosystem sensitivity can coincide with these community shifts. In chapter 3, I found just that: the loss of sensitivity in tallgrass prairie to precipitation amounts (year to year variability) occurred when species abundances were similar to those existing under ambient precipitation. This loss of sensitivity could have been due to either co-limitation by nitrogen, an

important nutrient for growth in this as well as the majority of ecosystems (Vitousek & Howarth, 1991; Blair, 1997), or to productivity reaching maximum growth capacities under extreme wet conditions. However, after the plant community shifted to a more mesic assemblage, sensitivity to precipitation levels was restored suggesting that either the traits of these more mesic species allowed for fuller exploitation of increased soil water levels through higher growth rates, or that they were able to circumvent co-limitation by nitrogen through higher nitrogen use efficiencies.

The above findings do not coincide with a number of large-scale spatial patterns that have shown decreasing sensitivity in more mesic systems compared with xeric systems (Huxman et al., 2004; Sala et al., 2012). One potential reason for the divergence from these patterns at within-biome and ecosystem scales could be the lack of large structural differences existing among ecosystems used in regional analyses (e.g., grass-dominated versus tree-dominated). A factor that often varies along with precipitation (and inversely to it) along a gradient of biomes is light availability. For example, in deserts there is very little canopy coverage, meaning light is not limiting for the majority of plants in this system. Alternately, forests have relatively high canopy coverage causing many more plant individuals to experience light limitation than in deserts; grasslands fall in between these two extremes as they typically have full canopy coverage but limited vertical structure. Co-limitation by light may be an important factor driving regional sensitivity patterns and may be why we do not see similar patterns at smaller scales. I do not suggest that sensitivity to chronic changes in precipitation will not adhere to regional models after sufficient time is allowed to result in full ecosystem transitions, just that shorter-term sensitivity will likely be driven more by traits of the plant community than by co-limitation.

Aboveground versus belowground sensitivity – My second question focused on whether ANPP sensitivity is an acceptable proxy for that of BNPP, which has important implications for

predicting effects on ecosystem services such as erosion control and carbon sequestration. I found that the answer to this question depended on the ecosystem and likely the time scale under consideration. In chapter two, ANPP and BNPP sensitivities were ca. equal in northern mixed grass and tallgrass prairie, yet BNPP sensitivity was much higher than that of ANPP in semi-arid shortgrass prairie. These findings conflict with optimal allocation theory, which states that under conditions of high soil resources, allocation of biomass should favor aboveground growth (Bloom et al., 1985). Although I cannot identify the mechanisms behind this differential sensitivity, it could be due to plant strategies in these more xeric systems which tend to experience very high levels of inter-annual variation in rainfall (Knapp et al., 2015); in years of high resource availability, it may be beneficial for plants to allocate growth belowground to maximize resource capture in subsequent dry years. In tallgrass prairie, I found no differences between ANPP and BNPP sensitivities and also no differences in community composition during two years of irrigation, which suggests a lack of allocation responses of the existing plant community. Alternately, using the same study system (ca. 5 km distant) in chapter four, I looked at the long-term effects of irrigation on BNPP (among other things, see below), and I found substantially different sensitivities of ANPP and BNPP after 20+ years of chronic water additions and correspondingly shifted plant community composition. From this, I speculate that the differential ANPP and BNPP sensitivities in this system likely result from species compositional or from genotypic shifts, which have been previously documented in this system (Avolio et al., 2013).

These findings call into question the current use of both ANPP as a direct proxy for BNPP sensitivity, a concern previously presented by others (Friedlingstein et al., 1999), as well as simple biomass allocation models to estimate BNPP responses to altered precipitation amounts. I have shown evidence that allocation shifts do not occur ubiquitously across ecosystems, and when

differences in ANPP versus BNPP sensitivities do exist, they do not always align with the idea that allocation shifts to favor growth opposite to the location of the abundant resource (Bloom et al., 1985). Alternately I suggest that, instead of simply using carbon allocation scalars, incorporating plant community structure and the associated biomass allocation schemes into models may yield a more accurate (though admittedly more difficult) prediction of future BNPP responses to altered precipitation regimes in the absence of extensive BNPP data, which is exceptionally difficult to obtain.

Sensitivity of productivity and biogeochemical cycling – With my fourth chapter, I addressed the question of how the sensitivity of primary productivity impacts biogeochemical properties in the presence of simultaneous climate-driven ecosystem attribute changes as well as increased fire frequency, a scenario likely to be brought about in many systems during global change (D'Antonio et al., 1992; Dale et al., 2001). In a tallgrass prairie system infrequently burned previous to 1991, and in which annual fire was implemented in 1991, I found no change in total soil N after 20 years, and a substantial increase in soil C, despite almost complete loss of all aboveground biomass during annual fire events. However, I did find that the rate of C accumulation in irrigation areas was slower than in areas receiving ambient precipitation, and there was a negative trend in soil N over time. During an extensive sampling regime in 2013, I found that BNPP inputs were reduced in irrigated areas, aligning with an allocation shift to greater proportional aboveground growth, as well as slower turnover rates. Both of these factors likely limited the amount of C entering the soil and the higher proportion of aboveground growth under chronic irrigation may be contributing to N loss in the system.

The lack of evidence for model predictions of decreased N and C pools under more frequent fire, even after two decades, is likely due to a number of factors. First, background global change

factors may be influencing temporal patterns of N pools though increased N deposition rates (Goulding et al., 1998). Additionally, biomass allocation tends to shift to more belowground production under frequent fire (Johnson & Matchett, 2001; Koerner, unpublished data), which may increase C and N inputs as roots die and are incorporated into the soil. Thirdly, not all C contained in aboveground plant tissue is volatized during fire events, and some of the C left behind is difficult for microbes to break down, thus providing long turnover times of soil C and potentially stabilizing these pools (Knicker et al., 2012; Soong et al., 2014). Fourthly, N translocation strategies of species well-adapted to fire may also be limiting the loss of soil N. As burning events were always conducted in the spring, plants had plenty of time to relocate nitrogen from senesced leaf tissue into rooting structures (Vitousek, 1982). Also, I predicted an increased rate of C and N loss accompanying chronic irrigation due to decreased root:shoot allocation and the accompanied annual fire regime. I found general support for this prediction in that long term irrigation reduced the rate of carbon storage of this ecosystem, although even with this, C losses predicted by ecosystem models under annual fire regimes were still not borne out. However, I would like to note that although I show biogeochemical data from 20 years of experimental manipulations, C and N pools will likely continue to change over much longer timescales, so continued monitoring and experimentation should be a priority for informing ecosystem models. Also, non-linear temporal trends may be manifested in the future through phenomena such as threshold responses and state shifts, and should be considered when thinking about longer term responses.

In summary, I first conclude that the use of regional models of primary production sensitivity to altered precipitation regimes may not be appropriate when predicting ecosystem function responses for short and moderate time scales. Second, BNPP sensitivity does not always mirror that of ANPP and assuming allocation responds to maximize resource gain is not always a

good predictor of how BNPP will respond when not aligning with ANPP. Instead, predictions should be based on attributes of the plant community in combination with potential allocation responses. Third, although productivity responses are important in their own right as a provider of ecosystem services such as forage production and wildlife habitat, they only partially explain how carbon sequestering abilities of ecosystems will be affected under global change scenarios, and multiple aspects of global change must be considered to accurately predict future ecosystem states. Overall, I found the identity of the plant community is an important determinant of above and belowground sensitivity to changes in precipitation regimes, and the characteristics and alterations of these communities should be taken into account more fully when predicting sensitivity shifts and associated effects on ecosystem services in a changing world.

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APPENDIX I

Table A1-1. Precipitation statisitics calculated for each treatment in 2011 and 2012 as well as long-term precipitation data for Manhattan, KS (1960-2010), Miles City, MT (1960-2010), and Nunn, CO (1969 – 2010). Large and extreme events were defined as those equal to or greater than the 80th or 95th percentile event size, respectively, compared to long term data obtained through the United States Climate Reference Network (USCRN).

Year		Variable	Shortgrass			Northern mixed			Tallgrass		
			A	MS	FL	A	MS	FL	A	MS	FL
2011	Water additions	Total ppt (mm)	231.9	304.7	304.7	449.8	511.5	511.5	414.6	538.2	538.2
		Increase from ambient (%)	-	31.4	31.4	-	13.7	13.7	-	29.8	29.8
		Number of events added	-	13	5	-	11	4	-	12	5
		Mean size of added event (mm)	-	5.6	14.6	-	5.6	15.4	-	10.3	20.6
	Precipitation regime incorporating natural variation	PPT coming in large events (mm)	124.6	146.2	197.4	359.1	374.9	415.1	181.6	181.6	243.4
		PPT coming in extreme events (mm)	46.4	46.4	131.7	257.0	276.8	301.8	0.0	0.0	41.2
		PPT coming in large events (%)	65.1	55.3	74.7	88.6	80.3	88.9	54.0	39.5	58.1
		PPT coming extreme events (%)	52.5	38.0	70.3	63.4	59.2	64.6	0.0	0.0	9.8
		Number of events	11	23	14	18	28	22	19	31	23
		Number of large events	6	8	9	17	18	20	6	6	8
		Number of extreme events	4	4	8	8	9	10	0	0	1
		Mean event size (mm)	5.6	6.1	7.1	8.6	8.8	9.3	9.3	9.8	10.5
		Mean large (80th percentile) event size (mm)	20.8	18.3	21.9	21.3	21.0	22.2	32.6	32.6	34.5
		Mean cumulative dry days	12.4	5.3	9.8	8.8	4.5	7.7	7.0	4.2	6.3
2012	Water additions	Total ppt (mm)	134.9	196.5	196.5	127.1	194.3	194.3	327.5	440.8	440.8
		Increase from ambient (%)	-	45.7	45.7	-	52.9	52.9	-	34.6	34.6
		Number of events added	-	11	5	-	11	4	-	11	3
		Mean size of added event (mm)	-	5.6	12.3	-	5.6	16.8	-	10.3	37.8
	Precipitation regime incorporating natural variation	PPT coming in large events (mm)	92.5	92.5	154.1	37.4	37.4	105.2	261.5	261.5	400.7
		PPT coming in extreme events (mm)	52.6	52.6	107.5	15.6	15.6	71.6	238.8	238.8	378
		PPT coming in large events (%)	74.8	49.9	83.2	41.6	23.8	66.9	79.8	59.3	90.9
		PPT coming extreme events (%)	42.5	28.4	58.1	17.3	9.9	45.5	72.9	54.2	85.8
		Number of events	7	18	10	9	21	12	10	20	10
		Number of large events	5	5	8	3	3	6	5	5	7
		Number of extreme events	2	2	4	1	1	3	4	4	6
		Mean event size (mm)	6.2	6.2	8.0	4.5	4.91	7.15	15.6	14.7	21.0

	Mean large (80th percentile) event size	18.5	18.5	25.7	12.5	12.5	20.9	52.3	52.3	64.6
	Mean cumulative dry days	16.6	6.6	16.1	16.3	6.0	13.9	14.1	6.4	13.8
		Normal		Wet	Normal		Wet	Normal		Wet
Historical precipitation regimes	PPT coming in large events (mm)	147.0		260.7	129.7		219.6	235.4		528.8
	PPT coming in large events (%)	71.7		74.9	66.8		71.5	54.5		77.1
	Number of large events	8.14		13.8	6.9		11.9	6.4		12.0
	Number of events	11		18	10.6		18.0	21.3		23.6
	Mean event size (mm)	5.52		7.04	5.51		6.71	10.6		16.1
	Mean large (80th percentile) event size (mm)	18.0		18.9	18.9		18.5	36.5		44.1
	Mean cumulative dry days	11.1		7.1	12.9		7.6	6.0		6.0

APPENDIX II

Table A2-1. Model results comparing soil moisture values from repeated measures ANOVAs and multi-comparison of least squared means among treatments at the Central Plains Experimental Range (shortgrass prairie), Fort Keogh Livestock and Range Research Laboratory (Northern mixed prairie), and Konza Prairie Biological Station (Tallgrass prairie). Watering treatment did not have a significant effect on soil moisture across the entire growing season at the shortgrass or tallgrass sites so multi-comparison of least squared means are not shown.

	Precipitation pattern			Precipitation addition		
Effect	df	F value	*P*	df	Test statistic	*P*
Site	2	24.65	<**0.01**	2	24.65	<**0.01**
Treatment (Trt)	2	3.03	0.05	1	2.14	0.15
Site*Trt	4	5.51	<**0.01**	2	5.41	<**0.01**

	Shortgrass			Northern Mixed			Tallgrass		
Effect	df	Test statistic	*P*	df	Test statistic	*P*	df	Test statistic	*P*
Treatment	2	0.49	0.64	2	19.23	<**0.01**	2	0.67	0.57
A – FL	-	-	-	67	-4.98	<**0.01**	-	-	-
A – MS	-	-	-	67	-5.69	<**0.01**	-	-	-
FL – MS	-	-	-	67	-0.71	0.48	-	-	-

Table A2-2. Model results from repeated measures ANOVAs showing collective responses of aboveground (ANPP), belowground(BNPP), total net primary productivity (NPP), and belowground : aboveground (BNPP:ANPP) net primary productivity to water addition regardless of pattern (Precipitation amount) and water added in different regimes (Precipitation pattern). Data were collected during the 2011 and 2012 growing seasons at the Central Plains Experimental Range, Fort Keogh Livestock and Range Laboratory, and Konza Prairie Biological Station. Dashes indicate model results that are redundant between the two model types.

		Precipitation pattern			Precipitation amount		
Dep. Variable	Effect	df	F value	*P*	df	F value	*P*
ANPP	Year	1	9.19	**<0.01**	-	-	-
	Site	2	409.72	**<0.01**	-	-	-
	Site*Year	2	42.37	**<0.01**	-	-	-
	Treatment (Trt)	2	5.99	**<0.01**	1	11.09	**0.03**
	Site*Trt	4	3.70	**<0.01**	2	5.8	**<0.01**
	Year*Trt	2	3.72	**0.03**	2	4.94	**0.03**
	Site*Year*Trt	4	2.38	0.05	2	2.87	0.06
BNPP	Year	1	2.46	0.12	-	-	-
	Site	2	20.18	**<0.01**	-	-	-
	Site * Year	2	84.70	**<0.01**	-	-	-
	Trt	2	6.46	**<0.01**	1	12.92	**<0.01**
	Year*Trt	2	0.23	0.79	1	0.09	0.76
	Site*Trt	4	5.58	**<0.01**	2	10.40	**<0.01**
	Site*Year*Trt	4	0.92	0.45	2	1.82	0.16
	Depth	1	84.44	**<0.01**	-	-	-
	Year*Depth	1	9.82	**<0.01**	-	-	-
	Site*Depth	2	2.71	0.07	-	-	-
	Site*Year*Depth	2	1.43	0.24	-	-	-
	Trt*Depth	2	0.29	0.74	1	0.58	0.45
	Year*Trt*Depth	2	0.05	0.95	1	0.01	0.91
	Site*Trt*Depth	4	0.2	0.94	1	0.22	0.80
Total NPP	Year	1	2.95	0.09	-	-	-
	Site	2	422.43	**<0.01**	-	-	-
	Site*Year	2	90.62	**<0.01**	-	-	-
	Treatment (Trt)	2	10.94	**<0.01**	1	21.84	**<0.01**
	Site*Trt	4	9.06	**<0.01**	2	17.44	**<0.01**
	Year*Trt	2	1.23	0.30	1	0.18	0.68
	Site*Year*Trt	4	0.79	0.53	2	1.05	0.35
BNPP:ANPP	Year	1	1.13	0.29	1	1.13	0.29
	Site	2	25.80	**<0.01**	2	25.80	**<0.01**
	Site*Year	2	17.69	**<0.01**	2	17.69	**<0.01**
	Treatment (Trt)	2	1.42	0.25	1	2.79	0.10
	Site*Trt	4	1.79	0.14	2	2.73	0.07
	Year*Trt	2	0.61	0.55	1	1.20	0.28
	Site*Year*Trt	4	1.64	0.17	2	3.05	0.05

Table A2-3. Results from repeated measures ANOVA's examining productivity responses to precipitation pattern and water addition individually for the Central Plains Experimental Range (shortgrass prairie), Fort Keogh Livestock and Range Research Laboratory (Northern mixed prairie), and Konza Prairie Biological Station (Tallgrass prairie). Dependant variables are: aboveground net primary productivity (ANPP), belowground net primary productivity (BNPP), total net primary productivity (Total NPP), and the ratio of belowground to aboveground net primary productivity (BNPP:ANPP). The only significant interaction between Year and Trt was found at SGS. Deeper examination of ANPP in the two years at this site revealed a similar response pattern but temporal variation in the magnitude of response. Because the pattern of ANPP response was similar in both years and we were interested in overall responses, the two years were pooled using repeated measures ANOVA.

			Shortgrass			Northern Mixed			Tallgrass		
Dep. Var.	PPT variable	Effect	df	F value	*P*	df	F value	*P*	df	F value	*P*
ANPP	Pattern	Year	1	24.38	**<0.01**	1	18.3	**<0.01**	1	116.78	**<0.01**
		Treatment (Trt)	2	12.56	**<0.01**	2	0.09	0.91	2	6.26	**<0.01**
		Year * Trt	2	5.50	**<0.01**	2	2.00	0.15	2	0.29	0.75
	Addition	Year	1	24.38	**<0.01**	1	18.30	**<0.01**	1	118.77	**<0.01**
		Trt	1	20.54	**<0.01**	1	0.17	0.68	1	12.60	**<0.01**
		Year * Trt	1	10.58	**<0.01**	1	0.71	0.40	1	0.33	**0.57**
BNPP	Pattern	Year	1	6.12	**0.02**	1	121.39	**<0.01**	1	67.40	**<0.01**
		Trt	2	10.16	**<0.01**	2	0.83	0.44	2	4.25	**0.02**
		Year*Trt	2	0.98	0.38	2	0.52	0.60	2	0.21	0.81
		Depth	1	29.23	**<0.01**	1	10.87	**<0.01**	1	75.53	**<0.01**
		Year*Depth	1	2.73	0.10	1	8.09	**<0.01**	1	0.67	0.42
		Trt*Depth	2	0.24	0.79	2	0.14	0.87	2	0.43	0.65
		Year*Trt*Depth	2	0.445	0.64	2	0.02	0.98	2	0.58	0.56
	Addition	Year	1	6.12	**0.02**	1	121.39	**<0.01**	1	67.40	**<0.01**
		Trt	1	20.24	**<0.01**	1	0.95	0.33	1	7.26	**<0.01**
		Year*Trt	1	1.92	0.17	1	0.89	0.35	1	0.04	0.84
		Depth	1	29.23	**<0.01**	1	10.87	**<0.01**	1	75.53	**<0.01**
		Year*Depth	1	2.73	0.10	1	8.09	**<0.01**	1	0.67	0.42
		Trt*Depth	1	0.46	0.50	1	0.01	0.93	1	0.79	0.98
		Year*Trt*Depth	1	0.13	0.72	1	0.00	0.99	1	0.10	0.76
Total NPP	Pattern	Year	1	21.70	**<0.01**	1	135.39	**<0.01**	1	168.62	**<0.01**
		Trt	2	13.27	**<0.01**	2	1.57	0.22	2	18.85	**<0.01**
		Year*Trt	2	0.42	0.66	2	2.80	0.07	2	0.05	0.82
	Addition	Year	1	21.70	**<0.01**	1	135.39	**<0.01**	1	168.62	**<0.01**
		Trt	1	26.31	**<0.01**	1	1.82	0.18	1	18.85	**<0.01**
		Year * Trt	1	0.16	0.69	1	2.62	0.11	1	0.05	0.82
BNPP:ANPP	Pattern	Year	1	1.71	0.20	1	30.22	**<0.01**	1	9.61	**<0.01**
		Trt	2	2.53	0.09	2	0.25	0.78	2	1.81	0.18
		Year*Trt	2	2.20	0.12	2	0.36	0.70	2	0.05	0.95
	Addition	Year	1	1.71	0.20	1	30.22	**<0.01**	1	9.61	**<0.01**
		Trt	1	4.57	**0.04**	1	0.34	0.57	1	1.53	0.22
		Year * Trt	1	4.35	**0.04**	1	0.26	0.61	1	0.09	0.76

Table A2-4. Comparison of least squared means of 2011-2012 ANPP, BNPP, and total NPP among treatments at the Central Plains Experimental Range (shortgrass prairie), Fort Keogh Livestock and Range Research Laboratory (Northern mixed prairie), and Konza Prairie Biological Station (Tallgrass prairie). The treatments at Fort Keogh did not result in significant effects within the overall model at the $\alpha = 0.05$ level so multi-comparison results are not shown.

		Shortgrass			Northern Mixed			Tallgrass		
Dep. Variable	Treatment comparison	df	t value	*P*	df	t value	*P*	df	t value	*P*
ANPP	A – FL	48	-5.00	**<0.01**	-	-	-	48	-2.87	**<0.01**
	A – MS	48	-2.89	**<0.01**	-	-	-	48	-3.23	**<0.01**
	FL – MS	48	2.14	**0.04**	-	-	-	48	-0.36	0.72
BNPP	A – FL	48	-4.03	**<0.01**	-	-	-	48	-2.89	**<0.01**
	A – MS	48	-3.76	**<0.01**	-	-	-	48	-1.74	0.08
	FL – MS	48	0.27	0.79	-	-	-	48	1.17	0.25
Total NPP	A – FL	48	-4.68	**<0.01**	-	-	-	48	-3.84	**<0.01**
	A – MS	48	-4.20	**<0.01**	-	-	-	48	-3.61	**<0.01**
	FL – MS	48	0.48	0.63	-	-	-	48	0.34	0.74

Table A2-5. Model results from repeated measures ANOVAs comparing sensitivity (productivity response in treatment plots minus paired control plots divided by amount of precipitation added) in the full model and split by site. Data were collected during the 2011 and 2012 growing seasons at the Central Plains Experimental Range, Fort Keogh Livestock and Range Laboratory, and Konza Prairie Biological Station. Bold P values are those < 0.05.

Full model				**By site**	**SGP**		**NMP**		**TGP**	
Effect	df	F value	*P*	Effect	F value	*P*	F value	*P*	*F value*	*P*
Site	2	9.60	**<0.01**	Year	3.53	0.07	1.87	0.18	2.53	0.12
Year	1	0.80	0.37	Type	11.04	**<0.01**	1.47	0.23	0.01	0.92
Year*Site	2	3.53	**0.03**	Year*Type	12.57	**<0.01**	0.02	0.90	0.00	0.96
Productivity type	1	1.40	0.24	Trt	0.03	0.86	0.47	0.50	0.24	0.63
Site*Type	2	6.14	**<0.01**	Year*Trt	0.35	0.56	0.92	0.34	0.07	0.79
Year*Type	1	4.77	**0.03**	Type*Trt	0.28	0.60	0.26	0.61	0.57	0.45
Year*Site*Type	2	4.17	**0.02**	Year*Type*Trt	0.13	0.72	0.32	0.57	0.06	0.81
Treatment (Trt)	1	0.02	0.89							
Site*Trt	2	0.38	0.68							
Year*Trt	1	0.79	0.38							
Year*Site*Trt	2	0.43	0.65							
Type*Trt	1	0.10	0.75							
Site*Type*Trt	2	0.42	0.66							
Year*Type*Trt	1	0.00	0.96							
Year*Site*Type*Trt	2	0.30	0.74							

APPENDIX III

Supplementary information 1. Data set descriptions

Irrigation Transects (IrrT) – First, ANPP and plant species composition data from an experiment conducted from 1991-2011 which irrigated plots weekly from May-September to remove all water limitation – based on weekly potential evapotranspiration estimates –resulting in significant increases in soil water content in the top 15 cm (Knapp, Briggs, and Keolliker 2001). Water was applied via sprinkler heads placed 1 m from the ground 10 m apart along a water line that transported water from a nearby ground-water well. At the beginning of the experiment, only one pair of transects (parallel watered and control plots) were present, but in 1993 the treatments were expanded to include another pair of transects. The amount of water added to manipulated plots during this period ranged from 53 to 469 mm with a mean of 256 mm across all years while the percentage increase relative to ambient ranged from 5.6 to 119.2 % with a mean of 46.4%. Although this experiment spanned a slight topographic gradient, we only utilized IrrT data from plots in a lowland area with finely textured soils (n = 9 for both watered and control plots).

Upland-lowland Comparison (ULC) – To examine the effects of a monotonic shift to drier soil water conditions, we used ANPP and plant species composition data from transects (n = 4) which extended from upland areas with shallow soils to lowland areas with deep soils in a watershed burned annually since 1972 and ungrazed for over 40 years. Plots in the transects located on the slope between shallow and deep sites were removed for all analyses.

APPENDIX IV

Table A4-1. Model results from repeated measures ANOVA using unstructured co-variance matrix and data from IrrT experiment and ULC data. Shows the main and interactive effects of experiment, treatment (or topographic position), and year on log-transformed aboveground net primary productivity (ANPP), graminoid production, and forb production. SAS code used is included below table. Degrees of freedom are listed in the form: numerator d.f., denominator d.f.

	FULL MODEL		ANPP			Graminoid			Forb	
	Variable	Df (n,d)	F	P	df(n,d)	F	P	df(n,d)	F	P
	Experiment	1, 365	65.37	<0.01	1,333	10.7	<0.01	1,150	5.95	0.02
	Treatment (or Topo)	1, 336	0.51	0.47	1,79.6	2.02	0.16	1,185	3.09	0.08
	Exp*Trt	1, 365	398.7	<0.01	1,333	392.8	<0.01	1,150	0.03	0.86
	Year	27, 26.6	19.95	<0.01	27,27	30.48	<0.01	27,29.7	3.78	<0.01
	Year*Experiment	19, 34	4.70	<0.01	19,34.4	6.31	<0.01	19,40	3.67	<0.01
	Year*Trt	27, 26.6	2.61	<0.01	27,27	3.52	<0.01	27,29.7	1.17	0.33
	Year*Experiment*Trt	19, 34	1.93	0.046	19,34.4	2.42	0.01	19,40	1.28	0.25
	BY EXPERIMENT		ANPP			Graminoid			Forb	
	Variable	Df (n,d)	F	P	df(n,d)	F	P	df(n,d)	F	P
Irrt	Treatment	1,15.1	38.3	<0.01	1,15.1	39.5	<0.01	1,15.1	0.1	0.75
	Year	20,300	14.1	<0.01	20,300	54.5	<0.01	20,300	4.42	<0.01
	Trt * Year	20,300	9.55	<0.01	20,300	19.2	<0.01	20,300	1.12	0.33
ULC	Treatment	1,6	74.1	<0.01	1,6	121.2	<0.01	1,6	0.47	0.52
	Year	26,156	31.05	<0.01	26,156	45.08	<0.01	26,156	4.72	<0.01
	Trt * Year	26,156	3.14	<0.01	26,156	1.92	<0.01	26,156	1.60	0.04

* Compound symmetry covariance structure

Table A4-2. Results from permutational MANOVA testing for differences between treatments or topographic position simulating chronically increased water availability (IrrT) or chronically decreased water availability (ULC) for each year of the experiment or in which data were available. Bolded values indicate significant differences between community centroids at $\alpha = 0.05$.

	IrrT		ULC	
Year	Psuedo-F	P	Psuedo-F	P
1983	-	-	**9.064287**	**0.001**
1984	-	-	**11.69818**	**0.001**
1985	-	-	**13.36419**	**0.001**
1986	-	-	**10.08548**	**0.001**
1987	-	-	**8.48367**	**0.001**
1988	-	-	**5.660682**	**0.002**
1989	-	-	**6.605513**	**0.002**
1990	-	-	**6.083309**	**0.001**
1991	0.376017	0.947	**9.47953**	**0.001**
1992	0.256573	0.964	**8.088501**	**0.001**
1993	0.616507	0.68	**13.11703**	**0.001**
1994	0.63053	0.749	**9.176693**	**0.001**
1995	0.683508	0.652	**8.007068**	**0.001**
1996	0.925828	0.477	**10.07767**	**0.001**
1997	0.960888	0.403	**12.99303**	**0.001**
1998	1.040658	0.386	**13.52317**	**0.001**
1999	1.699272	0.179	**13.07841**	**0.001**
2000	**2.82401**	**0.016**	**11.26638**	**0.001**
2001	**3.902915**	**0.008**	**10.4806**	**0.001**
2002	**3.196188**	**0.006**	**11.67677**	**0.001**
2003	**2.94854**	**0.009**	**10.85962**	**0.001**
2004	2.146528	0.052	**12.76159**	**0.001**
2005	**2.218731**	**0.017**	**13.27571**	**0.001**
2006	**3.318595**	**0.01**	**14.16384**	**0.001**
2007	**3.191399**	**0.002**	**13.35114**	**0.001**
2008	**2.616253**	**0.017**	**13.11606**	**0.001**
2009	**4.235377**	**0.001**	**15.30441**	**0.001**
2010	**2.701305**	**0.008**	**19.8347**	**0.001**
2011	**3.678488**	**0.001**	**20.54265**	**0.001**

Table A4-3. Results from a similarity percentages analysis examining species most contributing to differences between centroids of control vs chronically irrigated plant communities, and upland vs lowland in an annually burned, ungrazed watershed at Konza Prairie Biological Station. Species composition data from 2000-2011 were pooled and examined collectively for this analysis. Species shown cumulatively explain 90% of the variance between control and irrigated communities. Columns represent (from left to right): species ranked by level of contribution to divergence, average relative abundance in control plots or lowland (proportion), average relative abundance in watered or upland plots (proportion), average Bray-Curtis dissimilarity across all pairs of sites, average dissimilarity divided by the standard deviation of these dissimilarities across replicates, percent contribution of the species to divergence between groups, cumulative percent contribution (Clarke and Gorley 2006).

	Species	Cont. avg. rel. abun.	Wat. avg. rel. abun.	Av. Diss.	Diss ./ SD	Contrib. (%)	Cumul. (%)
Irrigation transect	*Panicum virgatum*	0.21	0.37	8.82	1.52	19.75	19.75
	Andropogon gerardii	0.38	0.31	7.45	1.38	16.69	36.44
	Schizachyrium scoparium	0.1	0.02	4.86	0.83	10.87	47.31
	Helianthus rigidus	0.02	0.07	4.1	0.6	9.18	56.49
	Dalea candida	0.04	0.05	2.9	0.81	6.49	62.98
	Lespedeza capitata	0.03	0.04	2.43	0.79	5.44	68.42
	Sorghastrum nutans	0.05	0.05	2.08	1.21	4.66	73.08
	Lespedeza violacea	0.04	0	2.02	0.35	4.53	77.61
	Solidago missouriensis	0.04	0	1.79	0.48	4	81.61
	Ambrosia psilostachya	0.02	0.02	1.38	0.7	3.09	84.7
	Solidago canadensis	0.01	0.01	0.92	0.52	2.06	86.76
	Amorpha canescens	0.01	0.01	0.9	0.53	2.02	88.77
	Aster ericoides	0.01	0	0.56	0.39	1.26	90.03

	Species	Lowland rel. abun.	Upland rel. abun.	Av. Diss.	Diss ./SD	Contrib (%)	Cumul (%)
Upland Lowland Comparison	*Panicum virgatum*	0.22	0.03	10.06	1.34	21.68	21.68
	Schizachyrium scoparium	0.17	0.28	7.78	1.43	16.76	38.44
	Andropogon gerardii	0.31	0.31	7.35	1.34	15.84	54.28
	Sorghastrum nutans	0.11	0.1	2.38	1.01	5.12	59.4
	Ambrosia psilostachya	0.04	0.03	2.04	0.79	4.38	63.78
	Amorpha canescens	0	0.04	1.8	0.91	3.88	67.66
	Salvia azurea	0	0.03	1.4	0.48	3.03	70.68
	Aster ericoides	0.01	0.02	0.92	0.55	1.98	72.67
	Psoralea argophylla	0.02	0	0.89	0.3	1.92	74.58
	Bouteloua curtipendula	0	0.02	0.82	0.81	1.77	76.35
	Dichanthelium oligosanthes	0.01	0.01	0.64	0.8	1.38	77.73
	Carex spp.	0.01	0.01	0.63	0.53	1.35	79.08
	Vernonia baldwinii	0.01	0.01	0.61	0.92	1.32	80.4
	Carex heliophila	0	0.01	0.59	0.63	1.26	81.66
	Solidago canadensis	0.01	0	0.58	0.35	1.25	82.91
	Baptisia bracteata	0.01	0.01	0.58	0.78	1.25	84.16
	Koeleria pyramidata	0	0.01	0.56	0.59	1.21	85.37
	Ruellia humilis	0.01	0.01	0.55	0.89	1.19	86.56

	Asclepias verticillata	0.01	0.01	0.5	0.78	1.08	87.64
	Ceonothus herbaceus	0	0.01	0.47	0.36	1.01	88.66
	Schrankia nuttallii	0	0.01	0.42	0.34	0.91	89.57
	Sporobolus heterolepis	0	0.01	0.39	0.43	0.84	90.41

Table A4-4. Univariate ANOVA results comparing relative covers between treatments or topographic position of the five most influential species contributing to differences between centroids between communities

					Treatment/ topo comparisons		
Experiment	Species	TRT	LS mean	SE	Df.n/df.d	F	P
Irrt	ANGE*	C	.381	0.03995	1/16.8	1.87	0.19
		W	0.3183	0.03995			
	SCSC*	C	0.09771	0.04009	1/15.2	2.59	0.13
		W	0.03186	0.04009			
	PAVI	C	0.1951	0.02523	1/21.1	26.73	<0.01
		W	0.3514	0.02523			
	DACA*	C	.03159	.02280	1/22.7	1.00	0.33
		W	.05119	.02280			
	HERI*	C	.02883	.02935	1/22.8	1.10	0.30
		W	0.06307	.02935			
ULC	ANGE	U	0.3404	.01231	1/120	0.36	0.5473
		L	0.3299	.01231			
	SCSC	U	0.2432	0.01252	1/89.9	10.89	<0.01
		L	0.1848	0.01252			
	PAVI	U	0.04435	0.01914	1/45.5	42.07	<0.01
		L	0.2200	0.01914			
	SONU*	U	.1303	0.007011	1/146	0.08	0.7841
		L	0.1137	0.007011			
	AMPS*	U	.02614	.002659	1/180	0.26	0.6102
		L	.02879	.002659			

*Dependent variables were logit transformed when raw scale was non-normal but we report untransformed ls means and SE's – also, ar(1) covariance structures were used

Table A4-5. Univariate ANOVA results comparing relative covers between treatments or topographic position of the five most influential species contributing to differences between centroids between communities

General model						Multiple comparisons		
Experiment	Effect	Num df	Den df	F	P	Fxn type	t value	P
Irrt	Fxn type	3	64	1208.2	<0.01	C4 grass	1.56	0.12
	Treatment	1	116	0.00	0.98	Forb	-1.67	0.10
	Fxn*Trt	3	116	1.79	0.16	Woody	-0.24	0.81
						C3 gram.	0.30	0.77
ULC	Fxn type	3	433	6215.9	<0.01	C4 grass	-5.74	<0.01
	Treatment	1	433	0.00	1	Forb	1.65	0.10
	Fxn*Trt	3	433	16.26	<0.01	Woody	3.58	<0.01
						C3 gram.	0.51	0.61

* Irrt functional model was run with unstructured covariance matrix based on AIC criteria.

Table A4-6. Model results comparing mean ANPP and correlations of ANPP and growing season (May-Sept) precipitation for ambient plots from 1991-2011, irrigated plots from 1991-1999, and irrigated plots from 2000-2011. Mixed effects ANOVAs (IrrT) and general linear models (ULC) were used to determine whether slope of growing season precipitation and ANPP was significant, and repeated measures ANCOVA to look for differences among slopes when both were significantly greater than zero. Sattherwaite approximations of error were used to account for differences in variance among treatments.

Mean ANPP responses

Overall model				**Multiple comparisons**			
Effect	**DF num,den**	**F**	**P**		**Amb vs I_{91-99}**	**Amb vs I_{00-11}**	**I_{91-99} vs I_{00-11}**
Treatment	2,30.1	55.65	<0.01	DF	17.4	16	339
				t	-3.76	-7.71	-8.47
				P	<0.01	<0.01	<0.01

Annual variation

	Model	**Time**	**Treatment**	**Model coef.**	**Model SE**	**DF num;den**	**F value**	**P**
Irrigation transect	mixed effects ANO	91-11	Ambient	0.29	0.04	1;176	49.71	<0.01
		91-99	Irrigated	0.15 (n.s.)	0.10	1;68	2.16	0.15
		00-11	Irrigated	0.46	0.19	1;105	5.87	0.02
	Repeated measures mixed		*Irrigated vs ambient*					
			Effect	**DF num;dem**	**F**	**P**		
			Treatment	1;257	0.22	0.21		
			Precip	1;267	29.85	<0.01		
			Trt x Precip	1;267	2.17	0.14		
Upland lowland comparison	GLM	Time	**Topographic position**	**Model coef.**	**Model SE**	**DF num;den**	**F value**	**P**
		83-11	Lowland	0.30	0.08	1;106	13.00	<0.01
		83-11	Upland	0.30	0.07	1;106	20.18	<0.01
	Repeated measures mixed		**Effect**	**DF num;dem**	**F**	**P**		
			Topo	1;70.9	17.83	<0.01		
			Precip	1;78.8	22.24	<0.01		
			Topo x Precip	1;78.8	0.06	0.81		

APPENDIX V

Table A5-1. Results from permutational MANOVA tests comparing irrigated versus ambient plant species relative covers in the upland portion of the irrigation transects at the Konza Prairie Biological Station, Manhattan, KS, USA from 1991-2011.

Year	DF	F value	P value
1991	1	0.714831	0.646
1992	1	0.85767	0.605
1993	1	1.350487	0.177
1994	1	0.848414	0.601
1995	1	0.72997	0.67
1996	1	1.882473	0.049
1997	1	1.609208	0.129
1998	1	2.019847	0.039
1999	1	1.575125	0.113
2000	1	1.889534	0.087
2001	1	2.801555	0.005
2002	1	3.21857	0.003
2003	1	3.366749	0.002
2004	1	1.610931	0.119
2005	1	2.307181	0.061
2006	1	3.509733	0.005
2007	1	3.228972	0.008
2008	1	3.221491	0.012
2009	1	3.086667	0.022
2010	1	3.237622	0.034
2011	1	3.090638	0.011
2012	1	3.779266	0.016

Table A5-2. The 6 most important species (ordered by importance) contributing to differences between irrigated and ambient communities in each year 1996-2011 defined by similarity percentage analysis. The last column shows the collective variance explained by the 6 species each year.

	Species 1	Species 2	Species 3	Species 4	Species 5	Species 6	Collective contr.
1996	*A.gerardii*	*A.canescens*	*S.nutans*	*P.virgatum*	*S.canadensis*	*S.asper*	0.62
1997*	*A.gerardii*	*S.nutans*	*A.canescens*	*P.virgatum*	*S.canadensis*	*S.asper*	0.65
1998	*A.canescens*	*A.gerardii*	*P.virgatum*	*S.nutans*	*S.canadensis*	*S.scoparium*	0.68
1999*	*A.canescens*	*A.gerardii*	*P.virgatum*	*S.nutans*	*S.canadensis*	*S.scoparium*	0.72
2000*	*S.canadensis*	*A.gerardii*	*A.canescens*	*S.nutans*	*P.virgatum*	*S.scoparium*	0.72
2001	*S.canadensis*	*A.gerardii*	*A.canescens*	*P.virgatum*	*S.nutans*	*S.scoparium*	0.76
2002	*S.canadensis*	*A.gerardii*	*A.canescens*	*S.nutans*	*P.virgatum*	*S.scoparius*	0.79
2003	*S.canadensis*	*A.gerardii*	*A.canescens*	*S.nutans*	*P.virgatum*	*S.scoparius*	0.80
2004*	*A.gerardii*	*A.canescens*	*P.virgatum*	*S.nutans*	*A.psilostachya*	*S.canadensis*	0.71
2005*	*S.canadensis*	*A.gerardii*	*A.psilostachya*	*P.virgatum*	*A.canescens*	*S.nutans*	0.85
2006	*S.canadensis*	*A.gerardii*	*P.virgatum*	*S.nutans*	*A.canescens*	*S.scoparius*	0.81
2007	*S.canadensis*	*P.virgatum*	*A.gerardii*	*S.nutans*	*A.canescens*	*A.psilostachya*	0.76
2008	*S.canadensis*	*A.gerardii*	*P.virgatum*	*S.nutans*	*A.canescens*	*A.ericoides*	0.75
2009	*S.canadensis*	*A.gerardii*	*P.virgatum*	*S.nutans*	*A.ericoides*	*A.canescens*	0.80
2010	*S.canadensis*	*A.gerardii*	*P.virgatum*	*S.nutans*	*A.canescens*	*A.ericoides*	0.81
2011	*S.canadensis*	*A.gerardii*	*P.virgatum*	*S.nutans*	*D.oligosanthes*	*A.canescens*	0.83
2012	*S.canadensis*	*P.virgatum*	*S.nutans*	*A.gerardii*	*A.canescens*	*S.scoparius*	0.85

* Communities were not significantly different at $\alpha=0.05$ during these years